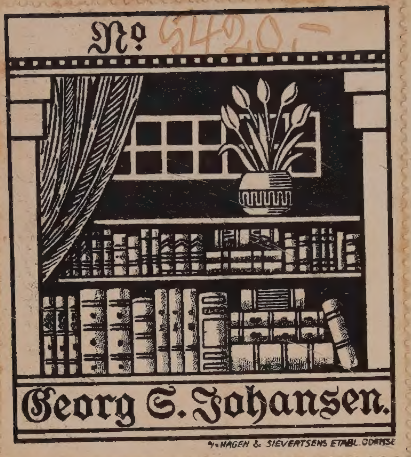
2468


No 5420.–
Georg S. Johansen.
HAGEN & SIEVERTSENS ETABL. ODENSE

R.F. Reiss
1959

375
11508

LINACRE COLLEGE LIBRARY
UNIVERSITY OF OXFORD

303215256R

150
JON

LINACRE
COLLEGE
LIBRARY

Presented by
R. F. Reiss
1989

THE MATRIX OF THE MIND

THE
MATRIX OF THE MIND

BY

FREDERIC WOOD JONES, F.R.S.

PROFESSOR OF PHYSICAL ANTHROPOLOGY, UNIVERSITY OF HAWAII
SOMETIME PROFESSOR OF ANATOMY IN THE UNIVERSITY OF
LONDON AND IN THE UNIVERSITY
OF ADELAIDE.

AND

STANLEY D. PORTEUS

PROFESSOR OF CLINICAL PSYCHOLOGY, UNIVERSITY OF HAWAII
FORMERLY LECTURER ON EXPERIMENTAL EDUCATION,
UNIVERSITY OF MELBOURNE.

LINACRE COLLEGE LIBRARY
UNIVERSITY OF OXFORD

LINACRE COLLEGE
WITHDRAWN

LONDON
EDWARD ARNOLD & CO.
1929

[*All rights reserved*]

Made and Printed in Great Britain by
Butler & Tanner Ltd., Frome and London

PREFACE

In the writing of this book the authors have had a very definite aim in mind, the blending of the subject matter and viewpoints of two sciences which have the same physical structures as a basis. These sciences are neurology and psychology. Too often the study of the structure of the central nervous system is conducted in almost total disregard of its higher functions. Similarly the ordinary text-book on psychology will contain a section dealing in more or less detail with the superficial anatomy of the brain together with some casual description of the cerebellum, the spinal cord and the sympathetic nervous system. But there is little or no attempt to relate structure to function and the book then proceeds with the discussion of sensation, attention, consciousness and behaviour in general as if these had no neurological basis whatsoever. Indeed some of the later text-book writers seem inclined to be quite frank in their ignorance of any connection between neurology and psychology and propose to treat the mind as if it were no more closely connected with the brain than with the larynx. On the other hand the anatomist's interest ends with the description of the component parts and ground plan of the machine with little regard to the plan in being, the whole machine at work. Yet the mind really has a brain and the brain a mind.

Because of the particular purpose of the book some of the theories which are intended to bridge the gap between the two sciences are, as it were, thrown in suspension, but in the present state of our knowledge we must be content with working hypotheses in the absence of conclusively demonstrated facts. Whilst every portion of the book has been the subject of the fullest discussion between the authors, each is entirely responsible for his own part. Chapters I to XLIII, dealing more particularly with the developmental story of the brain, is the contribution of the author (F. Wood Jones) having the more special anatomical training; the remainder, treating of the evolution of human behaviour, is the work of the co-author (S. D. Porteus), whose interests are mainly psychological.

FREDERIC WOOD JONES.
STANLEY D. PORTEUS.

Honolulu, Hawaii.

CONTENTS

PART 1

CHAP. PAGE
I Sensation and Movement 1
II Sensory and Motor Nerve Cells 9
III Appearance and Behaviour 15
IV Intuition and Panache 20
V Mistakes in Brain Building, and Cytoclesis . . 25
VI Moving Forwards and Making a Brain . . 35
VII Linkages and Neurobiotaxis 40
VIII Limitations and the Relevant Stimulus . . 48
IX The Rise of the Pallium 56
X Surface and Volume 64
XI Structure and Folding 70
XII Structure and Function 77
XIII Order in Representation 85
XIV The Rise of the Smell Brain 93
XV The Fall of the Smell Brain 100
XVI Linkages and Failures 110
XVII Sensation—Lowest Sensory Neuron . . . 120
XVIII The Second Sensory Neuron 128
XIX The Highest Sensory Neuron 135
XX The Thalamus and Sensation 140
XXI Informative Areas 146
XXII The Pallium and Awareness 150
XXIII The Acquirement of Awareness 154
XXIV The Pallium and the Body 159
XXV The Pallium and Movement 166
XXVI Movements amd Muscles 170
XXVII The Upper Motor Neuron 174
XXVIII The Corpus Striatum and Its Private Path . 183

CHAP. PAGE
XXIX The Labyrinth and Its Private Path . . . 189
XXX Muscles and Movement. 195
XXXI What the Cortex Cannot Do 203
XXXII The Cerebellum and Its Private Path. . . 208
XXXIII Changes in Level 215
XXXIV Movement and Education 221
XXXV The Brain and the Hind Limb 227
XXXVI The Lower Motor Neuron 233
XXXVII The Control of the Viscera. 238
XXXVIII Sound and the Brain 247
XXXIX Auditory Associations 253
XL The Photostatic System 260
XLI The Elements of Vision 264
XLII Completed Vision 272
XLIII The Triumph of the Pallium 283

PART II

XLIV Our Original Equipment 289
XLV Biological Pathways 297
XLVI Senses and Sensitivity 306
XLVII Facilitation 314
XLVIII Stimuli and Responses 328
XLIX Built-in Habits 342
L Preparing for the Cortex 354
LI Neural Cross-roads. 365
LII Monotony and Interest 372
LIII Sense of Aliveness 384
LIV Enjoyment and Appreciation 396
LV The Cortex and Intelligence 404
Index 420

THE MATRIX OF THE MIND

PART I

CHAPTER I

SENSATION AND MOVEMENT

The idea of a division of labour is a very old theme. We all know that with complexity of function there comes about complexity of structure. Labour is divided. One function belongs to one structure and another function is relegated to some other portion of a complex organism. But, in the beginning, we may expect to see a synthesis, we may look to find labour undivided and united in a very simple structure.

In a living animal organism that consists of a single cell, this cell must subserve the two great functions which are concerned in the manifestation of life: the cell must be sensitive and it must be capable of movement. An amoeba—a single living cell—is sensitive to a stimulus; it is capable of responding to the stimulus by the production of a movement. The single cell, which constitutes the animal, is sensitive and can move: it is, in itself, the receptor of sensation and the effector of movement. It is in its functions both sensory and motor.

But, with advance in structure, animals become multicellular, and with the elaboration of their bodies there comes the division of labour. In multicellular animals, in which the body is made up of a complex, into which a great number of cells enter, there are cells differentiated as those which are receptors of sensation or are sensitive and those which are effectors of movement or are motile. The two factors, at first combined in a single cell, are now lodged in different cells—there has been a division of labour.

There is a beautiful gradation shown in this business of specialization. Differentiation takes place in the cell as a unit, before it is manifest in the animal body as a whole. In the common Hydra there are cells known as *musculo-epithelial* cells which would be better termed *musculo-sensory* cells since that part of them which is exposed on the surface is sensory and that part which penetrates into the deeper tissues is motor (see Figure 2). The sensory portion of these cells is spread out as a surface layer in contact with outside stimuli: the motor part consists in contractile processes thrust into the deeper layers of the body wall. Here the two functions are combined in the single cell, but specialization has started. When specialization is complete the single cell of dual function becomes the dual cells of single function. The one cell retains sensation and remains upon the surface, the other retains mobility and is buried beneath the surface.

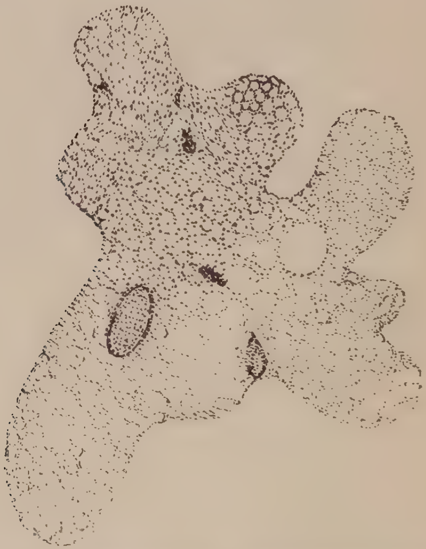


FIGURE 1.—An Amoeba, a simple unicellular animal capable of movement and sensitive to stimuli.

The cells which are specialized by their sensory qualities are those that are in the way of being subjected to outside influences. They are the cells that rub shoulders with the outer world; the cells that are specially sensitized to outside things and influences; the cells which have contact with the world without, as it is represented by the external environment of the animal. It is doubtless a misapplication of terms to speak of cells that know, or cells that have experience of the outside world, but there is in this specialized sensitiveness to outside things an adaptation of conditions that prompts the use of a terminology more expressive than exact. The surface of the animal which is turned towards the world is that part of it which may receive external stimuli. A knowledge of the environment comes from the environment, from without the animal body. It comes to those surfaces and parts of the body that are exposed to the outside world. The cells which compose this outer covering of the body are those to which this information is imparted, and they may be said to be the agents that are specially sensitized to the environment, and evidently they can hand the stimulus on to other parts of the multicellular body. Now if the sensitive cells of the outside of the animal body can gather sensory stimuli from the outside environment, it is not difficult to see how, in a very simple type of animal, they could hand this stimulus on direct by imparting it to a cell which, itself insensitive to outside conditions, could, nevertheless, produce movement. In such a case the cell which is the receptor of sensation could hand on the stimulus, by protoplasmic contact, to the cell which was the effector of move-

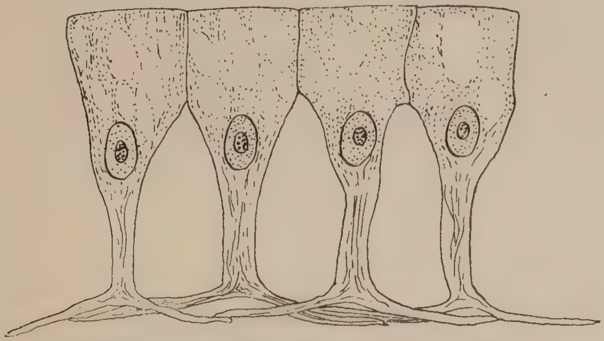


FIGURE 2.—Four musculo-epithelial cells of Hydra. The upper sensory parts are exposed on the surface: the lower parts are motile in function.

ment. The surface cell would exercise its special function as a sensory receptor, and, by protoplasmic contact, could hand on a stimulus, resulting from this sensation, to a cell, which, although having no dealings with the outer world, is capable of contracting and thereby producing movement. In such a simple case, therefore, we are dealing with a cell whose birthright is a sensitiveness to the stimuli derived from the outside world, which, receiving a stimulus from the outside world, hands on this stimulus to a cloistered cell whose only aptitude is that it can move. The cells of the whole of the exterior of a simple form of life are sensitive and each may impart the result of sensitiveness to an adjacent cell, which, lying beneath the surface, feels not, but can act.

Now it is certain that this very simple state of affairs can only be effective in an animal form of very simple organization. As the organization becomes more complex, the cells of the surface which are sensitive cannot hope to maintain contact with the deeply situated cells which act; they will inevitably become separated from them by the intervening tissues of the increasingly complex body. We stand in need of a further division of labour, for a middle-man is wanted; some go-between, which can still keep up communication between the sensitive cell of the surface and the acting cells of the deeper parts of the body. Some cells must be set apart for this task; and the selection naturally falls upon the cells which are sensitive. Some cells, which have as their birthright a sensitiveness to the outside world, must give up contact with the world and, still retaining their sensory nature, keep touch with their receptive fellows of the surface on the one hand, and with their acting partners on the other. They must wander from the surface, where they are begot, and take up their station in the tissues of the body: they must send out protoplasmic processes to maintain contact with their fellows at the surface and other processes to preserve the linkage with the deeper-moving cells (see Figure 3). These cells which have renounced the world, and with their worldly heritage have become cloistered in the tissues of the body, are *nerve* cells in their simplest form, and their protoplasmic processes are primitive *nerves*. We may term these pioneers *intercalated cells* and lay it down as an axiom that no matter what may be the complexity of the central nervous system it is always in essence an aggregation of intercalated cells.

By thus effecting a division of labour we have achieved a complex into which a sensitized cell which is on the surface, a nerve cell which has wandered in from the surface, and a moving cell deep in the tissues of the body, enter. This complex has been produced by the sinking in of certain cells, and, in the simple case we have been picturing, this sinking in has taken place in no definite or ordered manner. No special area of the surface of the animal has been selected for providing the cells that are to leave the surface and become nerve cells.

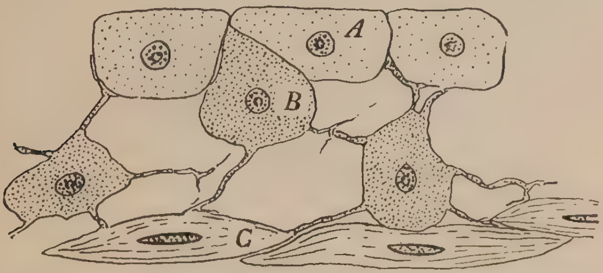


FIGURE 3.—Diagram to show the insinking of the surface cells (B) to maintain connection between the cells remaining at the surface (A) and the deeply-seated muscle cells (C).

When we come to such an ordered mechanism as is the body of an animal more complex than a Hydra (see Figure 4) this haphazard sinking in of surface cells will not suffice: not only are nerve cells wanted, but their ordered arrangement is necessary. A definite part of the surface must be set aside from which their invasion of the body is to start, and their invasion must be so managed that, when it has been effected, they constitute within the body a definite entity—the *nervous system*.

Here is a choice offered to the animal type; what area of its surface shall it elect to set aside for this purpose of providing cells which are to make an ordered invasion of its body? In all animal types the election has not been the same; some have chosen one area, some another. With us, and with all the members of our phylum, the choice, strangely enough, has fallen upon that strip of the surface of our bodies which runs down the middle of our backs. When we speak about the origin of our central nervous system as being from a *neural groove* situated in the midline of the dorsal aspect of the embryo, we must not forget that this is only another way of saying that in our phylum it is the fashion to tuck in a strip of the skin of the back in order to make a central nervous system (see Figure 5). Instead of the individual surface cells, which are sensitive, sinking in haphazard, it has come about that a strip of our surface (comprising myriads of cells which are sensitive) extending from head to tail down the middle of our backs, sinks in as a groove, which in the end becomes a sunken tube, to constitute our nervous system. If we inquire why

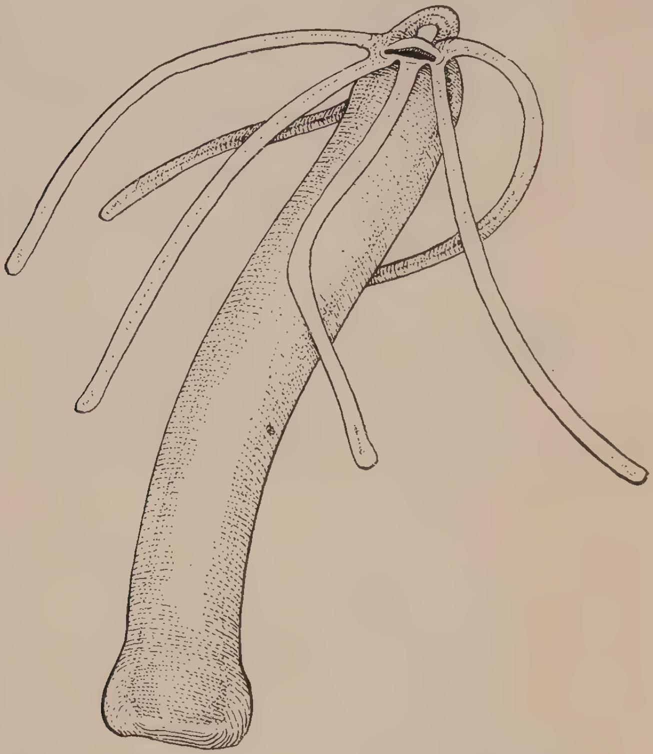


FIGURE 4.—A simple coelenterate type represented by *Hydra viridis*.

it is that we turn in a strip of the skin of the mid-line of our backs to form our central nervous system we are faced with a problem to which there is no very definite answer. We might hazard the explanation that the mid-line of the back of the developing embryo is an area in which nothing else is happening and that, therefore, it might be spared for this business. We might imagine that since the lateral margins of the body have already been dedicated to the production of limbs, there is little but the back and the front to choose from. But such is a poor explanation of a happening so vastly important as is the making of a nervous system. Be it the explanation or not, the fact is that adown the mid-line of the back of the embryo, where nothing else is happening, the skin tucks in as a groove, the groove deepens, its sides meet and it becomes a complete tube, and finally the tube becomes buried in the tissues in the body. This groove, which ultimately be-

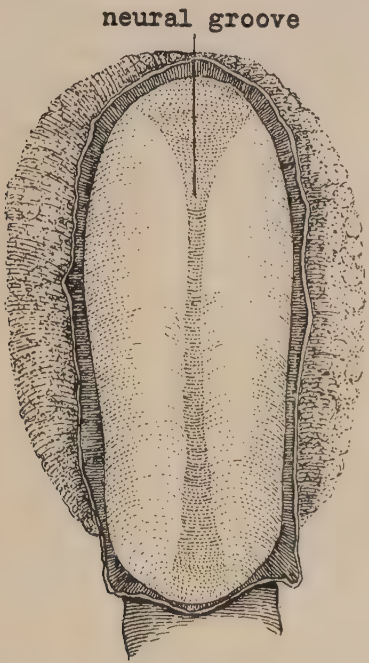


Figure 5.—The dorsal surface of an early human embryo. The neural groove is open in the whole of its extent and is considerably wider at the head end of the embryo.

comes a buried tube, is made of, and lined by, cells which are the sensitized cells of the surface of the body. It is the skin of the back which is infolded. It is the cells of the skin of the back that constitute our nervous system. Our brain, our spinal cord, our nerve cells and our nerves are in reality no more than skin cells of the middle of our back tucked into the depths of our body. They are tucked in because it is their birthright to be sensitized to the outer world and they are needed to interpret the stimuli derived from the outer world to the inner moving cells of the body that are cut off from the things of the world and yet are servants of a body that must perpetually adjust itself in response to the demands of its environment.

CHAPTER II

SENSORY AND MOTOR NERVE CELLS

When, in the developing human embryo, the nervous system makes its first appearance it does so in the form of a specialization of the surface of the embryonic body in a strip down the middle of the back. This strip is a part of the general surface of the outside of the embryo the rest of which will form the ordinary skin covering of the adult body. This long strip of specially sensitized cells becomes sunk in along the mid-line of the back. Soon its margins become elevated as ridges and these help to deepen it so that it forms a gutter. Finally, the upstanding edges meet above the gutter and convert it into a complete tube; a tube that is lined inside by cells of the surface of the body; a tube that has sunk right into the substance of the body and lies beneath the skin from which it came. In its final form this tube becomes encased in bone for its protection, and develops into the brain and spinal cord wrapped around and enclosed by the skull and vertebrae. Now this is a wonderful thing, that a gutter should be made of nothing more than the skin of our backs, that it should sink into the body as a tube, and then, preserved from injury by a casing of bone, become our brain and spinal cord. The skin of the back seems such a strange thing of which to make a nervous system; but it must be remembered that the skin of the back is made of cells which are specially sensitized to the environment and cells, which possessing this property, can be spared to elaborate and go through their evolutions in a region in which no other disturbance is taking place. It is a quiet region, and one not otherwise occupied: maybe that is why the great task of forming the nervous system is given over to it. But apart from the wonder of the thing as a whole there are the curious speculations, which a consideration of the process, as it affects the individual cells, must call forth. In a very narrow linear strip down the middle line of the embryonic back there are myriads of surface cells. If we take a cell which is situated absolutely in the middle line we may say its fate is certain. It is quite sure to be involved in the formation of the gutter; it is certain to be enclosed in the tube. There is no escape for it, it is destined to become a nerve cell, its chance of remaining as a skin cell is gone for ever. Although it has the birthright of being sensitized to the outside world, its fate is sealed; for inevitably it will become a buried nerve cell and lose contact with the world. We might speak of the cells of the absolute mid-line of the embryonic back as cells whose fate was predestined. We might also, having regard to the great continuity of life, say that they were cells well used to the business of being tucked into the body with all their attributes: that they were well used to the business of handing on stimuli to the cells that move but are not sensitive. But, if we take the case of the cells situated some way out on either side of the middle line the matter is not so simple, their fate is not so certain (see Figure 6). As the ridges rise up along the margins of the gutter, the cells which face inwards to the gutter will be shut up in the tube as nerve cells, while the cells which face outwards on the ridges will be left on the surface of the back as skin cells. Here then is a curious thing; for some cells adown the crest of the ridges it must be touch and go if they are to be turned in and become nerve cells, or left outside and remain as skin cells. Here apparently is chance in the life of the cell. This way or that, a microscopic margin, and it is to be a nerve cell, one of the most wonderful of living things, or to remain as a skin cell with no more apparent mystery than that entailed in forming a part of the ordinary covering of the back. Chance as it comes into the life of an individual appears almost trivial when comparison is made with this microscopic manifestation of what appears to us to be mere luck in the shaping of cell destiny.

When chance has had its sport and has tucked into the tube the cell of the top of the ridge, and left outside its next-door neighbour, the new-made nerve cell enters on a new career. But it is certain that, if we may consider the cell of the absolute mid-line as one well used to the business, this cell of the margin of the crest may be regarded as one new to the job. The cell of the mid-line is one that, in the whole long sequence of life, has lost its contact with the outer world the longest; but the last included cell of the ridge is one that only by chance loses immediate touch with the world; indeed but for chance it would still be part of the skin. The cell of the mid-line is one that has become most accustomed to dealing with the unknowing, moving cell in the depths of the body ; the cell farthest from the mid-line has no ancestral participation in these dealings. There is, therefore, a difference in quality of the cells from the mid-line to the margins of the groove, a difference in quality in the cells from the ventral side to the dorsal side of the tube when once it has been closed in and sunk into the body. This difference in quality initiates our next division of labour. The cell last tucked in as the most recent recruit to the central nervous system is in close structural and functional kinship with the cells of the surface which it has only just left: the cell first tucked in is in closer harmony with the moving cells and better fitted for dealing with them. The cell last tucked in, the cell

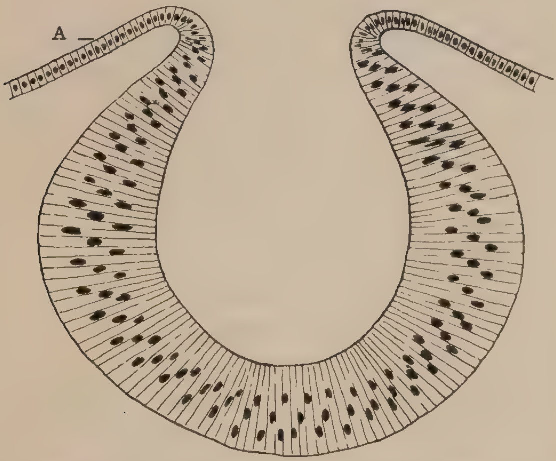


Figure 6.—Diagram of a section across the neural groove before the neural crests have met to form the tube. The general skin surface of the dorsal region of the embryo is seen at A.

of the margin of the neural groove, the cell of the dorsal aspect of the neural tube, is therefore specialized to receive the stimuli from the sensitized cell and becomes a so-called *sensory nerve cell.* These stimuli it hands on to the cells first tucked in, the cells of the middle line of the neural groove, the cells of the ventral aspect of the neural tube, which, therefore, become specialized for handing on the stimuli to the muscles and become *motor nerve cells.* We have now a complex of sensitized skin cell, sensory nerve cell, motor nerve cell, and acting cell; and all linked together by protoplasmic processes, *sensory nerves* on the one hand and *motor nerves* on the other.

It was in 1822 that the French physiologist Magendie, after a vast amount of research, gave to the world his fundamental dictum that the anterior or ventral roots of the spinal nerves were motor and the posterior or dorsal roots were sensory in function (see Figure 7). Now the anterior roots of the spinal nerves are the protoplasmic processes of nerve cells situated in the so-called anterior horns of the spinal cord. These nerve cells of the anterior horns are those of the ventral surface of the neural tube, those of the middle of the groove. They are the cells which phylogenetically have a long history of dealing with the acting cells and it is no wonder that they and their protoplasmic processes are motor in function. The posterior roots of the spinal nerves are, in the same way, the extensions of the last recruited nerve cells of the dorsal part of the tube, they are the protoplasmic processes bringing messages from the sensitive skin to the cells which have so recently left the surface to be enclosed in the back part of the neural tube. It is natural that they are sensory in function.

Although, stated thus, the whole affair may seem comparatively simple, it must not be forgotten that it was necessary, in order to discover the truth, for giants in the study of structure and function to labour without cease before the light shone forth. Nor must it be forgotten that, once the discovery of the division of labour in the ventral and dorsal portions of the spinal cord and its issuing nerves was made, it opened up a new world in neurological science and the healing art.

We may say that a philosopher, who had a due appreciation of the remarkable individuality of the cell, could have postulated the functions of the various parts of the spinal cord from an abstract consideration of its development. But it required the painstaking experiments, it needed the giants of the times, to unravel the whole intricate thread; and when the thread was unravelled, a new era started, an era in which the healing art could help humanity in a way undreamed of before. The symptoms of spinal cord and nerve diseases could be understood, correct diagnoses could be made, and proper treatment could be applied. Humanity could be helped in its hour of need. Magendie is justly lauded; the discovery was his and was hardly won: but one may be pardoned for thinking that a philosopher, who had due regard for the cell and its potentialities, and knowing the development of the nervous system, could have made the same discovery whilst sitting over his fire of an evening. But with the statement that the anterior nerve cells and the anterior nerves of the spinal cord are motor in function; and the posterior nerve cells and the posterior nerves are sensory, the matter is not ended. In the anterior (cephalic) end of the neural tube, which forms the brain,

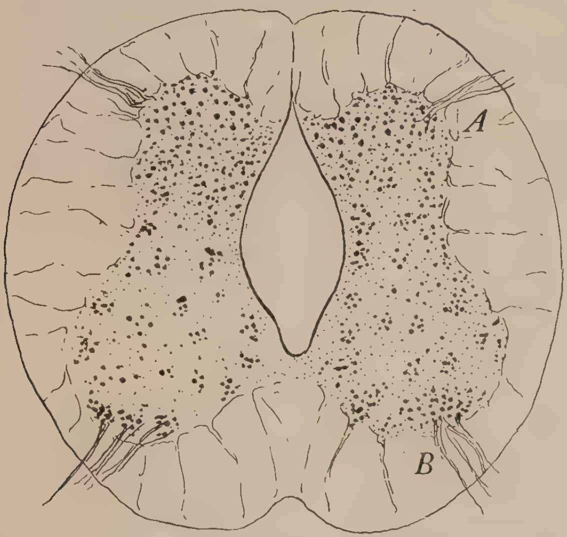


FIGURE 7.—Diagram of a section across the spinal cord. The posterior roots of the spinal nerves (sensory) are shown at A, the anterior (motor) roots at B.

the arrangement is naturally not so simple, for the tube has been distorted by the formation of the brain. But although the simple arrangement has been thus upset, we are still free to postulate that the nearer the middle line of the floor of the brain a collection of nerve cells be found, the more certain it is that they will be motor in function, and the farther from the middle line the greater their certainty of being sensory. The protoplasmic processes (or nerves) which emerge from the nerve cells of the brain, mostly take origin from what is termed in human anatomy "the floor of the fourth ventricle." Upon the floor of the fourth ventricle, the nerve cells towards the middle line are motor, those towards the sides are sensory in function.

In the spinal cord those on the front or ventral surface are motor and those behind are sensory; the tube has been more completely folded over in the spinal cord than in the region of the fourth ventricle.

CHAPTER III

APPEARANCE AND BEHAVIOUR

It is surely a strange thing that a part of our external surface should, during development, become buried in our bodies and tucked away inside a bony case as our brain and spinal cord. It is remarkable that our central nervous system should be made of buried skin; it is remarkable also that, conversely, our skin should be unburied nervous system.

One part of an original entity remains spread out on the surface of our bodies; the other part becomes buried within us as our brain and spinal cord. We might say that the nervous system was dual in nature, that there was an *external nervous system* consisting of our sensory skin and our sense organs, and an *internal nervous system* consisting of our brain and spinal cord: the two systems still linked by the protoplasmic bonds which are the nerves. For the man whose business it is to study his fellows, whether he does it as a physician or as a policeman, this conception may constitute a useful guide. It is well to remember that the outside of an individual, which we can see and examine, is in reality the spread out and exposed portion of that great system which is buried in the depths of the body and encased within the skull and spinal column and which is not open to our inspection. The outside of the body, or external nervous system, is what others can see, is in fact *what we look like*. The internal nervous system dictates our actions and our conduct and is in fact *what we are*. What we look like and what we are, are, therefore, dual parts of one integral whole. Regarded so, we may ask, is it strange we should look like what we are? There is truth, maybe, in the saying that beauty is only skin deep, but truth only when we regard the matter rightly. Beauty is deeper than the skin, for it is as deep as the central nervous system: but between the central nervous system and the skin there is that ancient kinship that may justify the saying.

For a moment we will leave the study of ourselves and turn to the case of some animals that we delight to term lower animals. If in our case our external nervous system is in accord with our internal nervous system it is likely that the same is the case with them. If our exterior is an index of our interior nervous system we might expect the same to be true in their case: but with them there is a vast range in the patterning, fashioning and colouring of the external surface of the body. It is this great variety of the exterior, manifested in lower animals, that in reality may make the matter clear to us. We all know of birds that are brightly coloured, gay in pattern, vivid in pigments: they have gay exteriors, gay external nervous systems. Are their internal systems likewise gay? May this gaiety be said to have a place in that which determines what they are: their brains and spinal cords? Such gaiety as may be said to reside in their brains and spinal cords will manifest itself in actions, in behaviour. Now here assuredly, though we leave arguments and speculations that may be termed scientific, we are, nevertheless, on safe ground. The bird that has a gay exterior has a behaviour entirely in accordance with his bright livery. The bird of bright plumage struts and displays himself, he parades and makes show, and indulges in actions and habits in accord with his bright exterior. Such conduct as is normal to him would be ridiculous in a bird not clad in his bright raiment. A robin has a scarlet patch upon his breast, his behaviour matches his badge of gaiety, of a surety we may say that in his central nervous system there is something that is attuned to this. A sparrow has a drab exterior, he has neither brilliant colour nor striking pattern in his plumage; has he also a drab internal nervous system? I think that we may presume this to be likely. The behaviour of a sparrow is drab. He may be said to have a dull grey-brown external nervous system and that which corresponds to dull grey-brown in his internal nervous system. He looks like what he is, or is what he looks like. Did we ever see a sparrow which perked and minced and flirted as a robin is wont to do? I doubt it; and if we did, the whole thing would appear highly ridiculous on the part of the sparrow. A sparrow has no equivalent to a scarlet patch in his central nervous system and to behave as though he had would be incongruous and absurd. Now, stated thus, the thing may appear to some to be fanciful: but taking the living world by and large I think its truth is manifest. When I see a grey gander mince and parade in his courtship like a peacock, when I see a drab lizard behave like jewelled *Amphibolurus* or when I watch an unadorned rat deport itself like an antlered stag in its pride of display, I may reconsider this dictum; but, until then, I think it is fair to maintain that the external appearance of an animal and its internal character, as manifested in its behaviour, are in wonderful accord. I think it is fair to say that the internal nervous system and the external nervous system show a wonderful harmony in the animal kingdom. If we admit so much it is possible that, accepting the inference only as an unproven but, maybe, helpful principle, we may go farther. The external nervous system—the exterior of an animal—is specially sensitized to its environment: the internal nervous system acts in harmony with the external nervous system, since with it, it is twin product of a whole. The external environment can react on the external nervous system, the function of which is to be sensitive to external things. The internal nervous system is only a part of a whole of which the other moiety is the external nervous system. The internal nervous system dictates what an animal is, and what its behaviour may be. Is it therefore a wonder that external environment, external characters of an animal, and animal behaviour accord somewhat closely?

Surely if biologists considered this sequence of events, some of their problems would receive an easier solution. The external environment impresses itself on the receptive external cells of the animal: it is the function of the external cells to be impressed by the environment. But some of the external cells have migrated inwards to become the central nervous system. These cells determine the behaviour of the animal. The environment may, therefore, influence the external and the internal nervous system.

Both external characters and behaviour may, presumably, be dictated by the environment, and an animal may fit its environment both in appearance and behaviour. It would seem that, by a very narrow margin of latitude this way or that, we might agree that the environment of an animal might directly influence both its external nervous system and its internal nervous system, might determine both its appearance and its behaviour.

Carried to these lengths, we might imagine that the environment could influence the external cells of an animal and so exert an influence upon its appearance, and that it might, at the same time, exert an influence upon its internal nervous system and so dictate its behaviour. And where in this is the inherent improbability? An animal that we deem to be well suited to its environment and has become, as it is termed, protectively adapted, behaves in accordance with this protection. There is no chance in all this. Structure and function are interdependent, and in these dual offsprings of one single cell layer, structure is manifested in the one as appearance and function in the other as behaviour. The functional behaviour is in accordance with the structural appearance. An animal that is protectively adapted behaves in accordance with its protective adaptation. There is no disputing this when we watch animals. We have only to observe the conduct of any animal which is protectively adapted to its environment to realize that the adaptation is not only in external appearance but in conduct and behaviour. For some, there has always been a factor lacking in any theory of evolution: there has been a failure to link environment, external characters and behaviour. Lamarck's *sentiment interieur* made the bond, but it was entirely vague. Surely in all this there has been some neglect to consider the respective rôles of the external and the internal nervous systems. That an octopus should settle on a rock, and change its outward appearance in harmony with the colour of the rock, is an evidence of adjustment between environment, sensitized cell and acting cell; a manifestation of the coordination of environmental stimulus, external nervous system, and internal nervous system. I imagine that few, after due consideration of a conception of the relation of external characters and internal nervous system, would deny some possibilities of harmonizing environment, appearance, and behaviour in the individual animal. That any should see a difficulty in transferring this conception from the individual to the race is merely the result of a half century of adherence to a definite creed—the non-inheritance of acquired characteristics. If we admit the harmony in the individual, and admit the possibility of the inheritance of the results of the working of this harmony, we have little way to go towards understanding those changes which we know to have occurred in the sequence of life.

Though, after reflection, adherence may be given to the doctrine that appearance and behaviour—structure and function—are interdependent, and though it may be conceded that, since these are the products of an entity, they may be regarded as inseparable; there is still a stumbling block for those who are unwilling to permit common experiences to rank as scientific data. Behaviour and appearance may be admitted to be merely two facets of a single entity, and there may be but little difficulty in conceiving that function may react upon structure, behaviour may influence appearance, and a close accord may, therefore, be found between the two. But the converse is not so simple a concept to the minds of some people. There may be difficulty in realizing that appearance may influence behaviour, though no phenomenon is more fully demonstrated everywhere in nature than that of structure influencing function. Even without having regard to animals, or to our fellow-men, we may make experiment in this; for there are few of us who are exempt from the urgings to nicety in conduct when under the tyranny of wearing our best clothes.

CHAPTER IV

INTUITION AND PANACHE

Returning to the study of ourselves, we have no patterned, pigmented, surface on which to display any gaiety that may be present in our central nervous system. We may hazard the speculation that did gaiety manifest itself in our external appearance in the form of colour and patches, it would accord with those areas of nerve distribution made familiar by the usual text-book charts of human segmental nerve distribution that depict the human skin as being patterned as strikingly as that of a zebra. If man ever did branch out into possessing a skin pattern on his surface, we would probably see these charts marked out on our patients, and clinical examination would thereby become more easy. As man is, he has lost this great field for the display of what he is. He has lost his ability to register on his skin any latent gaiety of his central nervous system: but he always has a hankering to regain this lost power. He may have to fall back on woad, he may have to daub himself with varied coloured ochres, or stick feathers to his skin. He may resort to dyeing his hair or tattooing his body or staining his finger-nails. These are all substitutes, and poor ones, for the great loss he has sustained in the inability of his external nervous system to express the hidden qualities of his internal nervous system. But it is over these very things that man, with his disabilities, rises superior to other animals. He can fall back on ornament and express himself in an artificial external nervous system known as garments. Dress and personal adornment—these are man's invention for displaying on his outside what may be the quality of his internal nervous system.

Dress and personal adornment are little more than a vicarious human external nervous system. And this is a subject which leads us far. Consider only the young man, who having that patch of gaiety in his central nervous system, which manifests itself in the robin as a scarlet breast on its external nervous system: that young man will wear a fancy waistcoat of some gay shade and, maybe, add to this expression by the addition of a daring tie. There is no more incongruity in one case than in the other, and I imagine that both are expressions of the natural relationship of the internal and external nervous systems. In a strange collection of child-words, known as the Berkshire gabble, is a term, invented by a little child, to express that type of man who, if he cannot wear everything brown, will certainly wear something brown. We all know that man. It is a legitimate speculation to inquire if this man who seeks expression in brown, sparrow-like, clothing does so because his internal nervous system is in accord. I certainly think that there are good grounds for suspecting that it is so.

When we speak thus of clothing we regard it more as an expression of the quality of the internal nervous system, than as a protection from the weather, or as a guarantee of modesty: and indeed we have much justification for so regarding it. Ornament is earlier than clothing. The paint and the shell necklaces of the Aurignacian culture paved the way for the bone sewing needle of the Solutrean. It would however be more in accordance with modern good taste to consider woman's love of dress as an expression of her innate modesty: but it would also be quite legitimate to speculate if it were not due to the fact that she is, at heart, a rake.

But apart from clothing, which is a human adventitious aid for displaying the qualities of the internal nervous system, we have admitted that our unclothed exterior is itself an outward manifestation of our inward qualities. We have admitted that, without clothes, our external nervous system is like to be akin to our internal nervous system: that we are wont to look like what we are. Most of us, in the everyday round, judge our fellow-men and women by their appearance. We assume that they are what they look like. At times we may be wrong; purely adventitious things may sway our judgment, but very often we are right. We may attribute some of our failures at least to the fact that human appearance is extremely complex just as is human behaviour. There are few people who are all good and fewer still who are all bad. It is so with appearance, one feature may belie the evidence of others, and many a man has a firm chin who lacks a firm character. A temporary upset of digestion may create an appearance out of accord with the normal behaviour. We are probably the more often right when we accept our first impressions of what another is like. We may be dissuaded from accepting our first impressions by certain extraneous circumstances: but first impressions, like womanly intuition, are notoriously often proved true. The intuition of women, as a rapidly drawn inference of what such a one is, deduced from what he looks like, is not to be despised. The shrewd judgments of children have their value. Great financiers, great leaders of men, great organizers of industry, have attained eminence in large part by what we term "a knowledge of men": they have shown an aptitude for estimating the qualities and characters of others, they have possessed a capacity which, though they would disclaim it as such, we will term a womanly intuition for detecting the harmony between the external nervous system and the internal nervous system. Though a financier, a leader, or an organizer, may become great and powerful by virtue of such an aptitude, no physician may even attain to mediocrity in the absence of this gift. Perhaps it would be more just to use the past tense and to say that no physician could formerly attain even to mediocrity: for in these days of instrumentation and bio-chemistry, a physician may achieve success, as such is accounted, without possessing any of the qualities which made, and which still make, the real physician. The older physicians were adepts at this business of correlating the appearance of a patient with the condition of his nervous system. They sought rather to learn what was the state of the central nervous system, what was the ease or disease of the individual, than what was the quality of the individual. If our mere skin-covered exterior may tell much, our sense organs may tell more, and, as we shall see later, the eyes have served a curious apprenticeship in their relation to the internal and external nervous systems. In what we look like, our eyes play great part; in the manner of their connection with both nervous systems they have especial privileges. It is not unnatural, therefore, that, even in the crudest and most popular expression of this thesis great value should be attached to the eyes in telling what we are. Now, man is by no means a simple animal and the very complexity of his nervous system may introduce an upsetting factor into all this. A robin behaves as he looks. He looks what he is. What he looks like and what he is probably do not concern him. But man knows of these things, he knows what he looks like, and there comes a time in his life when he knows what he is. To know what you are is not always pleasant. What we actually are, maybe, is not exactly what it would be best for us to be. The world at large, or our immediate surroundings, may expect from us some quality which we know full well we lack. It will at once occur to the individual that in order to preserve his harmony with his environment he must act as is expected of him and not as his nervous system dictates. We may, therefore, expect to meet with apparent contradictions in human appearance, individuality and behaviour.

Suppose we meet a man who, in every visible character, evinces a make-up that we would estimate belonged to a cut-throat. We may yet see that man deport himself like a school-girl and utter the sentiments of a young curate. These things do not invalidate our thesis—they would not deceive a woman who had intuition. The chances are that the man looks like a cut-throat and is a cut-throat; but knowing himself to be a potential cut-throat he hides his aptitudes in this direction under some other guise. We may know that we look meek and are meek; the more reason, therefore, to act as though we were bold. Many a one with a harsh exterior and with a harsh nature, from which sympathy is lacking, realizes the lack that is in him. It is this person, who would not feel a pang of sorrow at reading the obituary notices of yourself and the whole of your family, yet insists, at any chance meeting, on the most eager inquiries concerning your health, and that of your dear wife and the children. This is where man has introduced a complication into an otherwise very simple state of affairs. Being a sparrow and knowing he is a sparrow he yet may act the robin. Of a truth we may all wear a cockade. Where would most of us be in the esteem of our fellows did we not appreciate the proper employment of panache. It is for the student of his fellows, be he a physician or policeman, to discriminate between the panache and the patient.

CHAPTER V

MISTAKES IN BRAIN BUILDING, AND CYTOCLESIS

A nervous system is an all-important thing for an animal to possess. It is the nervous system which will one day stamp the rank of the developing phylum.

In all the story of animal progress nothing is so important as the development and perfection of the nervous system and every bit of cell energy and resource given up to its building is well repaid. There can be no turning back in the development of the nervous system if animal progress is to be maintained. Since there can be no turning back from the business of building, it would be imagined that, before laying the foundation stones of the structure, the whole plans of the edifice and the consequences entailed by its erection would have been well considered. But there are some very strange happenings in the development of the nervous system; events which seem to have been quite unlooked for or provided against when the business of building the system was started. Indeed the central nervous system may vie with the all-important reproductive system in manifesting those shifts that have been resorted to in order to escape from dilemmas imposed by what appear to us as unlooked-for consequences of change.

We have noted that, in order to make a nervous system, we and all the members of our phylum set aside a strip of the body surface along the mid-line of the back; but other animals have solved the problem differently. The invertebrate animals were faced with the same necessity of providing an area of surface from which to make a central nervous system and they elected to set aside a strip down the front, or ventral, surface of the body. In them the nervous system, when it is finished, is ventral to (below) the intestine, in us, when it is finished, it is dorsal to (above) the intestine. The same end is attained; a part of the surface has sunk in as a gutter and become buried; but in the two cases exactly opposite portions of the body were set aside to form the gutter. It might seem that since, in the elongated coelomate, the sides of the body were preempted as the sites for the limbs, there was an alternative choice of the quiet area of the dorsal surface or of the ventral presented for the area from which the neural tube could sink in. It is to be noted that there is no common meeting-ground for the vertebrate and the invertebrate; they constitute two independent phyla whose only common ancestor is to be found among the coelenterates. Both were faced with the problem of setting aside an ordered linear area of the surface for inclusion as the central nervous system and each phylum solved the problem in its own way.

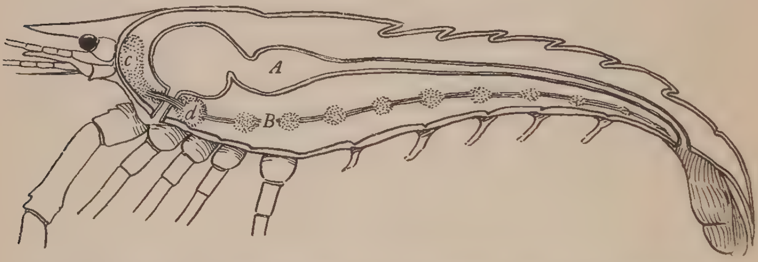


Figure 8.—Diagram to show the relation of the nervous system (B) to the alimentary canal (A) in an invertebrate. The supra-oesophageal ganglion is marked *c* and the infra-oesophageal ganglion, *d*.

In addition to that portion of the nervous system which is formed from a gutter down the front of the body and which remains ventral to the intestine, such invertebrates as possess adequate sense organs situated upon the dorsal aspect of the head set aside another field for the reception and co-ordination of their stimuli. This anterior field creates that portion of the nervous system which is dorsal and anterior to the intestine (see Figure 8). It forms the *pre-oral* or *supra-oesophageal ganglion* or collection of nerve cells, which may be said to constitute the cephalic part of the invertebrate's brain. But the posterior part of its brain is *post-oral* or *infra-oesophageal.* The oesophagus, therefore, in its passage from the mouth to the stomach, has to pass through the midst of the nerve masses that are aggregating to form a brain. Now here is a dilemma; the animal has built its brain around its oesophagus. What is to happen if its brain grows bigger, as brains must, if progress is to be maintained? If the brain continues to grow bigger, the oesophagus stands in danger of being compressed in the midst of the growing brain. As Gaskell has said "progress on these lines must result in a crisis owing to the inevitable squeezing out of the food-channel by the increasing nerve mass" (see Figure 9). And it would seem that the crisis actually came about, for "in the highest scorpion and spider-like animals the brain-mass has so grown round and compressed the food tube that nothing but fluid pabulum can pass through into the stomach: the whole group have become blood-suckers." To be-

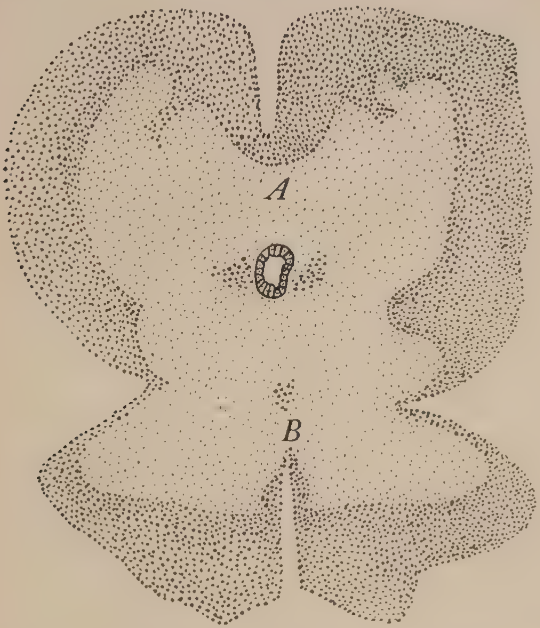


FIGURE 9.—Section across a well-developed brain of a young *Thelyphonus*, a scorpion-like invertebrate. Supra-oesophageal ganglion A. Infra-oesophageal ganglion B. The alimentary canal is represented by the small tube in the centre of the brain (after Gaskell).

come a blood-sucker is to become a failure. Phylogenetic senility comes with the specialization of blood sucking. Phylogenetic death is sure to follow. Here, then, is an end to the progress in brain building among the invertebrates. Faced with the awful problem of the alternatives of intellectual advance accompanied by the certainty of starvation, and intellectual stagnation accompanied by the ability of enjoying a good square meal, they must perforce elect the latter if they are to live. The invertebrates made a fatal mistake when they started to build their brains around the oesophagus. Their attempt to develop big brains was a failure, it resulted in inevitable starvation. Another start must be made.

This other start was the vertebrate's start. A new type of animal was tried, and, as the skin of the front or ventral surface had proved a failure, the skin of the back or dorsal surface was tried. But even this venture encountered a difficulty early in its career. We have described the area of the mid-line of the back as a quiet region in which nothing much was going on. But it was not quite an unoccupied region, for, at the advancing end of the body —the ultimate head end—there must be those special sensory areas which warn the animal of the world ahead of it. It must be remembered that it was these dorsal cephalic sense organs that had wrecked the progress of the invertebrate: for the most dorsal of the head sense organs had dictated the development of the supra-oesophageal ganglion. It is the most dorsal of the cephalic sensory areas which, strangely enough, came near to playing havoc with the vertebrate plan of brain building. Some of these areas might be right at the front, some far down on the sides of the head, but it might chance that some would be on that surface which would be involved in the formation of the neural gutter. These sensory areas are the specialized portions of the outer covering of the animal that will one day become organs of special sense, and they are known as *placodes*. These placodes are scattered about the head region to warn the animal of its surroundings as it advances through the world: and when they have taken on their adult stages in us they are known as the nose, the eye and the ear. It is with the placodes of the eye that some difficulty is encountered by the vertebrates (see Figure 10).

Obviously, as the head of the animal is the business end, more of the central nervous system must lie at this end, and the brain must be at the fore end of the advancing body. But to constitute so big a thing as the brain, a larger field of surface must be set aside to form the gutter of the nervous system at the front end of the body. This is the factor that creates the difficulty with the eye placodes. These things develop, like other placodes, as surface specializations of the outer covering cells of the body and of necessity they must be situated in a dorsolateral position upon the head of a primitive vertebrate that crawls upon its belly. The placodes for the eyes are first formed as surface thickenings upon the sides of the dorsal part of the head end of the embryo, and no sooner are they developed than they, and the surface area from which they arise, are commandeered as part of the area which is to be infolded to form that expanded part of the neural tube which will develop into the brain. Here then is a strange predicament. The eye placodes have been developed on the surface of the body in order that they may look outwards and appreciate visual stimuli from without. But the neces-

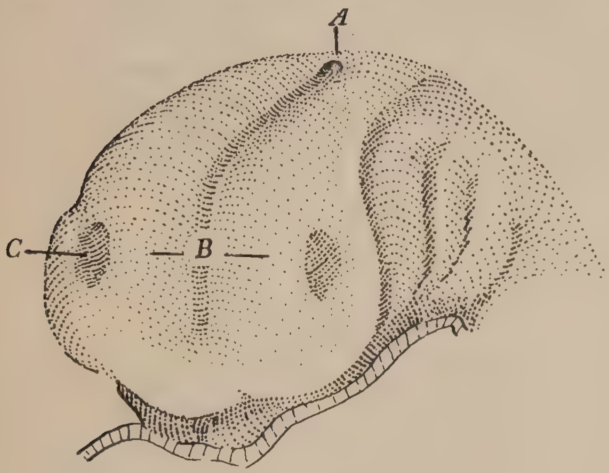


FIGURE 10.—The head end of a human embryo to show the relation of the optic placodes (C) to the neural groove, which is still open in the brain region (B) but closed further back (A).

sity for including a wide region of the surface of the anterior end of the body within the infolding area, has led to their being involved in the folding. When the process is complete and the gutter is transformed into a tube sunk below the surface, these placodes, intended to face the light of the outer world and so inform the animal of things visible without, are turned inwards so that they face into the centre of a dark tube sunk within the tissues of the body (see Figure 11). It would seem as though the necessity for reserving a large field of the outer surface of the body from which to make the anterior end of the nervous system had been of such paramount importance that it had been carried out regardless of the fate of the eye placodes. But here the vertebrates are in better case than the invertebrates. The invertebrates could not proceed with the development of a brain which necessitated the wreckage of the alimentary canal, for that meant death. The vertebrates, however, could proceed with the development of a brain which entailed no more than imperilling the eyes. Theirs was a problem that could be solved. And they solved it. In the solution of the problem there is manifested one of the most wonderful transformations seen anywhere in the processes of development. The imprisoned eye placodes, as soon as they are shut into the dark neural tube, begin to grow towards the surface of the skin again. They start off to regain the surface and the light, by growing out from the neural tube towards the skin of the future face. If we say that the optic placodes grow outwards, to constitute the optic cup, connected to the brain by the optic stalk, it may sound a simple enough process. But consider the marvel of it. A few cells, about to become specialized to the function of appreciating rays of light, are, by the adventitious circumstance that a large surface area is necessarily infolded in the cranial region, turned inwards and buried in the neural tube sunk within the tissues of the body. They appear to be influenced by their position and, at once, start to grow outwards towards the surface and the light. As they grow outwards, another marvel happens. They grow towards the under surface of what is the ordinary skin-covering of the face; but, as they approach the surface, the cells of the surface undergo a change.

Without entering into details, we may say that, as the imprisoned eyes grow towards the surface, the surface reacts and becomes transparent. What was the opaque skin, becomes transformed into the transparent cornea and lens and it transmits the light and focusses it upon the

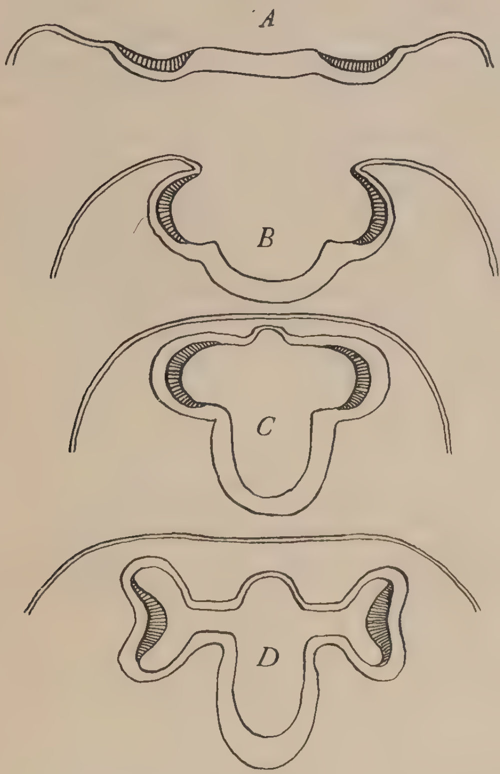


Figure 11.—Diagrams to show four stages in the development of the vertebrate lateral eyes. In A, the optic placodes are exposed on the surface of the neural groove. B, C and D show successive stages in their inturning and subsequent outgrowth.

sensitive imprisoned placode which is advancing towards it. This is a case of a set of cells (in this case the specialized cells of the retina of the eye) which when approaching other cells (in this case the cells of the overlying skin) appear to exert an influence upon them, appear to call to them to react. This phenomenon, the call of cell to cell, has been termed by the present writer *Cytoclesis*, and it is the concept that underlies the remarkable researches of Hans Spemann on the "organizers" of embryonic development.

The development of the eye affords a dramatic example of this phenomenon of cytoclesis, and the term is, therefore, introduced in connection with this striking demonstration of what is in reality a general factor in cell bionomics. The principle has been with us from the start, it will remain in action till the end. We have already seen it manifest in the wandering inwards of the cells of the external surface of the body to make links between the sensory skin and the deeper parts that move. It is cytoclesis that maintains the anatomical bond between the entities already bound by function. It is cytoclesis that determines that all cells subserving related functions may have the power to group themselves together to the end that the arrangement may be such that these functions are most advantageously discharged. It is cytoclesis that weaves structure and function together and we shall meet it at every turn in the building of the central nervous system. We shall meet it again under the guise of neurobiotaxis in the making of the brain stem, we shall find it again in the formation of the cortex. It may need a happening so strange as is the development of the eye to make the phenomenon real to us; but in truth it is displayed wherever cells are gathered together. The cytoclesis, which the imprisoned eye placode, approaching the surface, exerts on the surface cells, is a call that these cells should alter their position and their character: that they should start the ordered construction of a cornea and lens and become transparent in the process. That the call is one exerted by the outgrowing eye placode cannot be doubted, for in a tadpole the developing eye has been removed from its proper place and grafted under the skin of different portions of the body. The developing eye still gives forth its call and the surface cells respond in harmony. The call goes forth and is responded to with the production of a lens from the surface skin, even if the surface beneath which it is grafted be that of the abdomen instead of the head. But, though the developing eye possesses these strange powers, it is yet powerless to undo the original wrong done to it, when, as a placode, it was infolded into the dark neural tube. When it was a placode, formed on the skin of the head region, its cells, specially sensitive to light rays, formed a layer that was directed outwards towards what would one day be the aspect from which the rays of light would come. But as the formation of the gutter goes on and from the gutter the elaboration of the tube, the receptive surface of the placode is turned inwards and looks directly into the tube. From the tube it can and does again grow out towards the surface and the light; but as it grows, its receptive surface always faces into the tube and not towards the surface of the head. Imagine a fabric with a well-marked "right" side and "wrong" side, make it into a tube like a sleeve with the right side inwards. Now push out from within two lateral pouches like two fingers of a glove: the right side is still inside, the wrong side is still outside. The tips of these glove fingers reach a surface and impinge against it: but still they are wrong side out. In the outgrowing eye, the right side is represented by the placode cells which form the sensitive cells of the retina, the wrong side by the

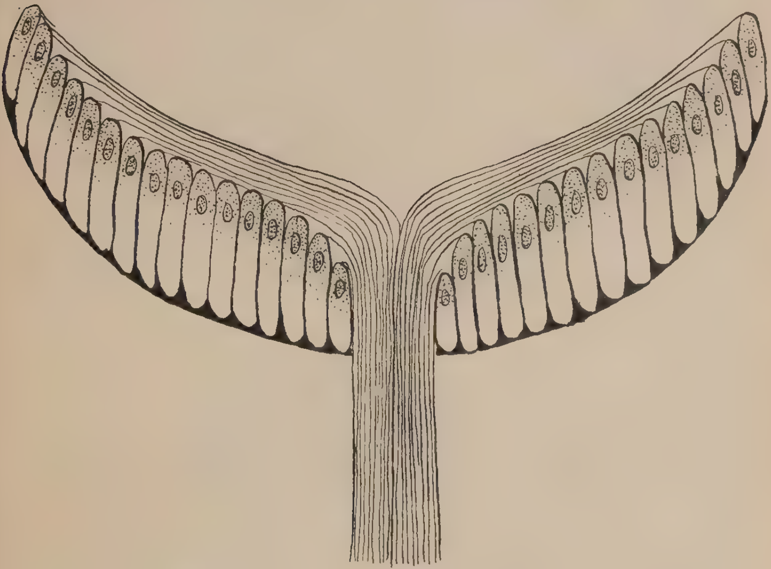


FIGURE 12.—Diagram of the inverted eye of a vertebrate. The nerve fibres intervene between the sensory retinal cells and the light.

protoplasmic processes or nerves which convey the stimuli from these cells to the brain. It thus comes about that our eyes are what is called *inverted compound eyes* (see Figure 12): or, as we might say, eyes with the sensitive parts turned wrong way round, because by chance, and in the ordinary process of making a brain from a dorsal surface area, they have become turned inside out. We have liberty thus to speak of them and there is no presumption in it, since the invertebrates possess several types of eyes which have not suffered this mischance of making and are not become turned inside out in their development; and, also, we might suppose that, as an optical apparatus, our eyes, turned inside out, in consequence of a primary mistake in brain making, are poor things compared with the *non-inverted or upright* eyes of the invertebrates (see Figure 13).

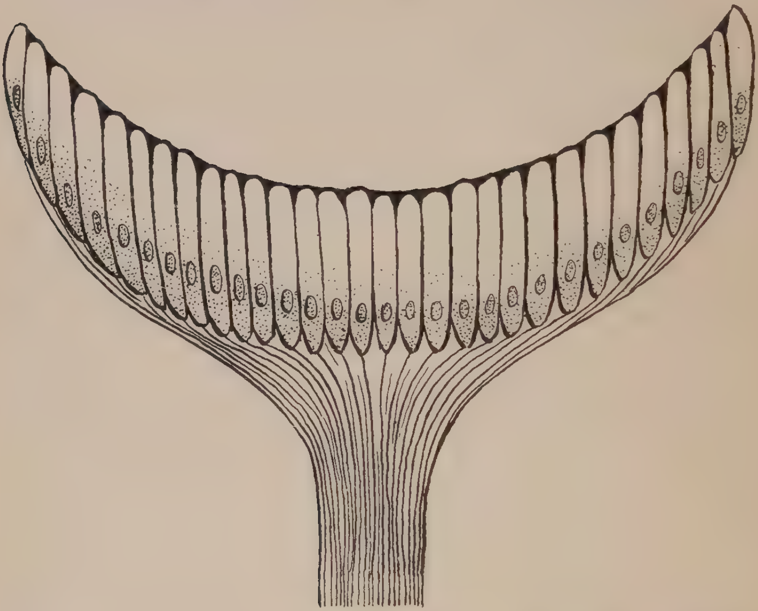


FIGURE 13.—Diagram of the upright or non-inverted eye of an invertebrate. The sensory cells of the retina are directly exposed to the light.

CHAPTER VI

MOVING FORWARDS AND MAKING A BRAIN

It is said that rolling stones gather no moss, and if the gathering of moss be a desirable thing presumably the loss is theirs. But it may not be agreed on all hands that it is well to gather moss, and it must be admitted that, if from stones we extend the saying to animals, we may at least assert that if rolling animals do not gather moss they are like to gather brains and that is much better for them.

I believe this expression is commonly extended from stones to animals and is commonly levelled against the young man who wishes to go to sea and visit foreign parts. I fancy, also, in this extension of the saying the term moss may be taken to include money or worldly goods or stake in the country or credit or something of that kind. That may or may not be true: it does not matter to us, but it is a poor ideal to inculcate into the youth of an insular race with a hankering after maritime enterprises. Maybe for a stone it is well to gather moss: I do not know. Maybe for a stone it is well to remain in one place and not to roll: it is not well for an animal to do this. Several have tried it and have failed. Picture an animal that, acting on the precept suitable to the stone and, remaining in one place, abandons all attempts at rolling and prepares to gather moss. An animal that remains fixed, has no special spatial relation to the world, the world is all round it, the world affects it equally on all sides. All sides are like to be developed equally as far as appreciating the outer world is concerned. There will be no fore end, no hind end, no sides to such an animal. It will be like to become developed into a form which presents on all sides surfaces having equal potentialities. It is like to become *radially symmetrical* (see Figure 14). But once an animal gives up this sedentary life, the life which gathers moss, and moves about the world, a change is certain to come about. As it moves through the world, and fails to gather moss, one end is in advance, the other end is behind. The end which moves forwards is the fore end, the end which follows is the hind end. For a radially symmetrical animal there seems to be no advance. If an animal elects to be sedentary, and to become adapted on all sides, equally, to its environment and adopt a radial symmetry, even though it may gather moss, there is no phylogenetic future. It remains inert, unprogressive and, as it does not advance as an individual, it will not advance as a phylum. But for the animal which proceeds through the world uniformly in one direction there is advance, advance for itself, advance for its phylum. The end of the animal which leads the way in its movement through space is the end that learns about the world. It

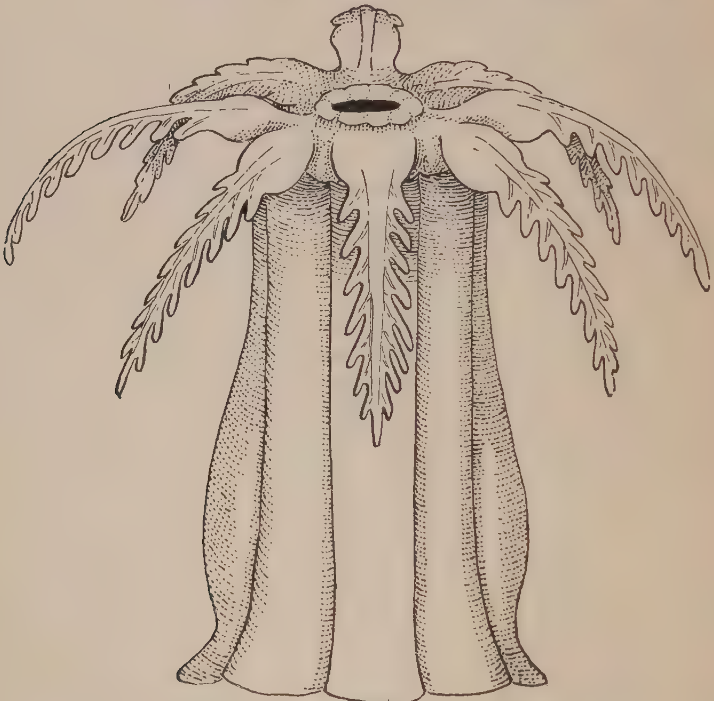


FIGURE 14.—An alcyonarian coral; a typical sedentary animal that displays radial symmetry.

is the business end; the end which bumps into outside things and learns about them: the end which makes new contacts with the world and informs the rest of the animal. It is, therefore, the end of the animal upon which the informative sense organs are developed. When we ask what is the range of informative sense organs that can be developed upon the advancing end of an animal we are limited for an answer to what we know concerning our own sense organs and those of animals sufficiently like us to guarantee an extension of our sensations to them and to their similar sense organs. We know that on our advancing end we can develop an organ capable of appreciating stimuli of touch, pain, heat and cold; a mere refinement and specialization of what we have as a common possession of the whole of our sensitive surface cells. We know that developed at the extreme front end of our bodies is an organ with a chemical sense capable of appreciating stimuli; in us an olfactory organ, which discriminates scents; but in other and aquatic animals, maybe, ministering to an allied but a different stimulus. There are sense organs developed at the advancing end of the animal body in order to be sensitive to light rays, such as in us can appreciate the limits of the wave lengths embraced within the visible spectrum. Again we know that we have sense organs developed in our anterior end for the appreciation of the air-borne sound waves: organs, again, which can interpret our movements and position in space, and organs capable of being stimulated by dissolved chemical substances and so of appreciating the taste of food or other material taken into our mouths.

When one end goes first, as an animal moves through space, these things all demand place at the advancing end. Waves of light and heat will be encountered by it. Waves of sound, chemical stimuli and stimuli of contact, pressure, pain and position will be imparted to it; and, since things which it must ingest for its nourishment will be met at its advancing end, it will have a sampling organ subserving in varying degree the senses of smell and of taste. These sensations come to the surface cells of the advancing end, they come to the ordinary sensitized cells of the outside of the body, and in order to appreciate them the surface cells become specialized. They form placodes, each placode being an aggregation of sensitized surface cells specialized and differentiated for the reception of some definite form of specialized knowledge. Of the whole gamut of ether-borne waves with which the advancing end of the animal is surrounded and which it encounters in its advance, we have developed placodes to appreciate a very limited number. We can appreciate the ether-borne waves of light within a short range of wave lengths from 400 to 800 millimicrons comprised by the visible spectrum: we can appreciate the air-borne waves within the comparatively short range of the frequency of 40 a second to 4,700 a second.

Outside these limits we are blind and deaf. Now, it cannot be too strongly insisted that though we can adjudicate for the sensory appreciations of other animals sufficiently like ourselves to warrant the extension of our sensory appreciations to them, we cannot adjudicate for animal forms so unlike ourselves that we cannot know either of their sense organs or of their sensations. This line of reasoning applies to the invertebrates as a whole. It is useless for a man to attempt to dictate as to what an insect appreciates and what it does not. An insect possesses sense organs unrepresented in us or in any vertebrate. We may know the young mother is wrong when she says her baby makes some response because the angels are whispering to him; we may guess that satisfactory peristalsis is at the root of it. We may be sure the spinster is incorrect when she diagnoses all the hidden meanings in Fido's actions: what she postulates to be anxiety on her account may be due to nothing more than the presence of ecto- or entero-parasites in the dog. But we cannot pretend —and it is better we should at once, and for all, give up the pretence—to understand what is affecting the pectinated antennae in a male moth during the marvellous phenomenon known to entomologists as "assembling." We cannot assume a knowledge of what affects the many sense organs of ants, and wasps and flies and spiders when they perform their marvellously intricate life rôles. We do not possess these sense organs and we cannot justly assume to know what they convey to the animals. When I see a dog sniff with his nose and respond by some action, I may properly infer that he acted in response to a stimulus which is like to that which I term "smell." But when I see a moth wave its pectinated antennae and then set out on a course of action, I have no sort of knowledge as to what stimulus made the moth act. I have no pectinated antennae and I have no knowledge as to what these things convey. But speculations, such as these, are like to lead us too far astray from the question of the rolling stone and the advantage of advancing, with one end constantly in front, through the world in which we live.

When we keep one end in front and move forwards, it is the front end that will receive the stimuli and will develop the sensory placodes. Since one end becomes the site for the development of all these things, it is obvious that, at this end of the body, there will be a maximum of cells set apart for the handing on of these stimuli to the acting cells of the animal. In other words, a larger part of the surface will have to be turned in to make the bond between the specially sensitized cells of the placodes and the acting cells of the body. The nervous system will, therefore, tend to be especially well developed at the anterior, advancing, end of the body. This is the beginning of the development of a brain. A brain is merely the cytocletic aggregation of a large area of inturned surface at the anterior end of the body called into being in order to deal with the greater number of stimuli imparted to the placodes of the anterior end of the body. The building of a brain has been a dangerous occupation. It has ruined the invertebrate stock: it has had perils for the vertebrate. The animal has had to pay for the luxury of possessing a brain. As we have already seen, this larger inturning of the surface has become so extensive that it has involved the eye placodes in the making of our brains. Fortunately the other placodes of our advancing ends are in no danger—else we might turn other things into the anterior end of our neural tubes. By advancing in one direction through our environment we have continued to roll and accordingly have failed to gather moss, but we have gained a head end; have gained a variety of cranial sense organs—efficient for us but, considered in relation to available stimuli, strangely limited; and having a head end, we have gained, what matters most of all, a brain.

CHAPTER VII

LINKAGES AND NEUROBIOTAXIS

The mid dorsal area has been set aside for the insinking of the nervous system. The neural gutter has been formed, the neural crests have risen up. The neural tube has been formed and has sunk into the dorsal part of the vertebrate body. Within the neural tube some cells have been detailed off as sensory cells to receive stimuli from their fellows left exposed on the surface, and some have become motor nerve cells to hand on the stimulus to the acting, moving, cells. All these stages we have seen in the making of a vertebrate nervous system. In the human embryo all these phases have occurred. The outside cells have been inturned. Sensory and motor cells have been differentiated; the sensory cells still in protoplasmic (nerve) contact with the outside cells, the motor cells in protoplasmic (nerve) continuity with the inner, moving cells. All is ready for the reception of stimuli from the outside, sensory, cells and for the handing on of these stimuli to the acting cells in order that, thereby, action may be produced.

Although it is necessary to make a rather well-defined distinction between motor nerve cells and motor nerves on the one hand and sensory nerve cells and sensory nerves on the other, we must not overlook the fact that all we have learned about their origin teaches us of their essential unity. It is a common function that provided that biological basis upon which cytoclesis wrought when it arranged the linkages between the units. The cell exposed upon the surface of the skin we may truly say is specialized as a sensory cell and the muscle cell is as truly motile: but the sensory nerve cell and sensory nerve and the motor nerve cell and the motor nerve have a common function that, in its essence, is neither sensory nor motor since it is merely that of transmitting what we term a stimulus. The stimulus is conducted from the surface cell to the muscle cell, but the intervening links are neither truly sensitive nor truly motor —they are the middle-men, the handers on and, one imagines, the transformers of the impulse which is nervous action. The impulse of the stimulus passes from the skin cell to the muscle cell, the stimulus that arises from the skin cell is of the nature that we are accustomed to term sensory; but when it has passed to the end plate of the nerve that connects with the muscle it produces a motor effect.

Now in all this it may be seen that though an efficient system has been created for the reception and the handing on of stimuli, it is all, so far, on rather a parochial scale. It is easy to see that if the outside cells of any particular part of the body receive a stimulus, this stimulus may be handed on to the sensory nerve cells and the motor nerve cells immediately subjacent to them. We might conceive that action in response to sensation might be appropriately, but still locally, carried out. We might extend this conception from a mere point on the surface which was sensitive and produced reaction, to a whole segment of the animal which was sensitive and handed on the stimulus and produced the response. Evidently we have to increase the protoplasmic linkage between the buried cells of the nervous system. A buried cell which has become a sensory nerve cell must have linkages with more than one motor nerve cell; it must translate multiple impulses and transmit them to multiple motor cells. This linkage is carried out by means of the development of many protoplasmic processes from each of the individual nerve cells. These processes are mere extensions of the cell, as the pseudopodia are of the body of the amoeba, and they make contact with other nerve cells in their neighbourhood (see Figure 15). By means of these processes, or *dendrons*, any individual nerve cell may make contact with, and hand on stimuli to, a wide series of adjacent nerve cells. In this way a stimulus imparted to a limited region may influence motor nerve cells capable of acting on muscle cells which can produce a complex action involving many moving parts. We might picture the beginning of the process in such an example as is seen in touching the outer surface of a sea anemone and watching the tissues withdrawn at the immediate site of contact. We might extend it to such a case as is demonstrated in touching the toe of a frog and watching it withdraw the leg. In the one case the response is local, in the other a local stimulus provokes a more than local response. It is easy to understand this difference. We have only to realize the more complex linkage of nerve cells, by the development of dendrons, to appreciate the more wide-spread response produced by the localized stimulus. But though it is easy enough to see how well such a system might work for a very simple animal—an animal simple both in structure and function—the limits of its successful working are also obvious. If we are dealing only with the stimuli of contact received by the ordinary surface cells, we can readily imagine the way in which the stimulus of a contact may be carried by dendrons to a large number of moving cells and so produce complex movements. But even here we have a difficulty, for not only must the stimulus be carried to many moving cells to produce complex movements, it must be carried to just those moving cells that can produce *appropriate* movements. It is not enough to produce a response: it must be an appropriate response.

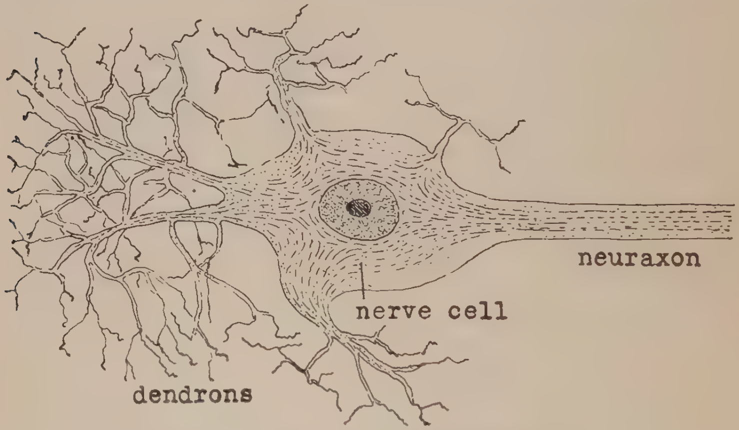


FIGURE 15.—The nerve cell and its processes.

Now when we come to an animal with definite cranial sense organs and a definite brain, the difficulty becomes far greater. We are dealing with complex stimuli, olfactory stimuli, visual stimuli, auditory stimuli and taste stimuli as well as with the stimuli of contact. Very varied response may be needed on the receipt of these varied stimuli, and though we can picture the production of varied response we are faced with the same problem, but on a far greater scale, for these varied responses must needs be appropriate. On the receipt of, say, a certain visual stimulus an animal needs to make some appropriate response. The dendrons of the sensory cells of vision must, therefore, form linkages, or *synapses*, with the dendrons of a definite series of motor nerve cells which can influence the muscles that are capable of producing this appropriate response. Another visual stimulus may demand another response, and still the response must be appropriate. The complexity of linkages by dendrons must needs be very great in the brain region to which the stimuli from the cranial sense organs stream. But something more than mere complexity is needed; some system is required; some power to ensure that incoming stimuli influence the proper sets of motor cells. It is easy to see that incoming stimuli might need to effect different appropriate movements in different animals. A movement proper in one animal upon the receipt of a certain visual stimulus, might be highly improper in the case of some other animal. To advance as the result of some visual stimulus might for one animal ensure a meal, for another it might mean certain death. There is, therefore, an increasing difficulty in conceiving the manner of linkages, for appropriateness is individual and linkages cannot, therefore, be carried out on a stereotyped base plan. The power which creates the linkages must be plastic.

In speaking of the development of the eye we noticed that curious phenomenon of cell call which we have termed cytoclesis. It was in this very business of making linkages between the myriad cells of the developing brain that the phenomenon denoted by the term cytoclesis was first recognized and given an accepted place among the recognized forces acting upon the cells of the developing embryo. In 1913, at the International Congress of Medicine, held in London, Ariens Kappers of Amsterdam first succeeded in making the bulk of English-speaking anatomists appreciate his conception of *Neurobiotaxis*. Neurobiotaxis is in reality nothing but a special manifestation of cytoclesis; it is simply a name for the call of cell to cell as it is demonstrated among the sensory and motor nerve cells of the developing nervous system. Neurobiotaxis is the force which, exerted by the sensory nerve cells, enables them to call to their side the motor nerve cells that are capable of influencing the muscles producing the appropriate response. Wherever an aggregation of sensory cells may be, to which sensations from without may stream, there will be, alongside them, the motor nerve cells which are capable of effecting the best, the most appropriate, and the proper response to the stimulus. In the developing brain these things are called together; the living, developing, sensory nerve cells call the living motor nerve cells and hold them by this strange force. All manner of change may take place around them, and yet this force, the neurobiotaxis of Ariens Kappers, holds them side by side. The sensory nerve cells call to the appropriate motor nerve cells and hold them whilst all else about them changes. As lovers they hold hands and thus remain, regardless of the world which moves around them. Now this is a marvel, a marvel when we picture the thing as a present happening, when we think of sensations already instreaming and motor apparatus alert for action. But the more is it a marvel when we realize that all is laid down long before the sensory stimuli arrive and before the motor apparatus is completed for producing the response.

There is a parallel to this in the case of the eye that we have already noted. The sensitive part of the eye buried in the neural tube grows towards the surface again—but it does not grow towards the light, it grows towards the surface upon which, in some distant day, the light will fall. The eye placode is inverted into the dark neural tube, it grows outwards, but it must be remembered that when this is happening, all is dark. The cornea and lens are formed in response to the cytoclesis exerted by the outgrowing retina; they are formed to transmit light, but there is no light when they are forming; they develop in the dark at a site where, at some future time, light will be. When a human embryo is three months advanced in development, the eyelids form and meet across the eye: in another four months the eyelids open again, for the human baby is born with its eyes open. But we must not forget that the eyelids form and close, close and open again, not because light rays reach them, but because one day light rays will fall upon them. All is done in the dark in the anticipation that one day the rays of light will shine upon the surface, pass through the transparent media and illumine the sensitive cells so that they may convey impressions to the brain. So it is with the neurobiotaxis, or cytoclesis, of the sensory and motor nerve ganglia. Sensations are not instreaming when the sensory cells call to the motor cells. The call is exerted in anticipation of sensory impulses which will one day come to the sense organs, and need to be handed on to the appropriate motor mechanism. If we take a new-born pup and put our finger-tip to its lips it will start the movements of suckling. The blind, helpless, staggering thing feels the sensation of its mother's nipple; it grasps it and the motor mechanism of suckling and swallowing starts forthwith. The instreaming sensory stimuli from the lips have passed the impulse on from their sensory nerve receptors in the brain to the motor cells which evoke the responsive movements in the muscles involved in suckling and swallowing. These sensory nerve centres and motor nerve centres were called together in the entire absence of actual, present, stimuli coming to the sensory cells. They were called together in the anticipation of the instreaming of these stimuli in the actual pup; but they did it on what may be conceived as the racial experience of millions of ancestral pups. The sensory cells which will one day receive the impressions from the pup's lips, called to their side the motor nerve cells in the brain of the developing pup, and they called to their side those motor nerve cells, which, in the accumulated experience of countless generations of ancestral pups, were capable of producing the most appropriate motor response. It is not the actual stimuli that, producing a call in the sensory cells, is the factor which effects the grouping of appropriate cells. The pup feels the nipple, it grasps it, it sucks and it swallows; because, long before these events were like to happen, all has been made ready by the grouping of nerve cells in its brain stem.

By neurobiotaxis things are arranged by cell call, and in the absence of actual, present contingencies, so that a blind and stumbling puppy suckles as apparently knowingly as did the myriads of those other puppies in its whole long line of ancestry. The human eye is made in the dark and carries out its destiny with an apparent foreknowledge of the inevitable ultimate presence of light. The sensory nerve cells to which the organ of sight is connected in the brain stem call to their side the motor nerve cells which dictate the movements of the eye and eyelids—and much more besides. In the developing brain stem the sensory centres of vision have these motor nerve cells (the cells of origin of the third, fourth and sixth cranial nerves) in chains. They have them as beads strung on a thread, all

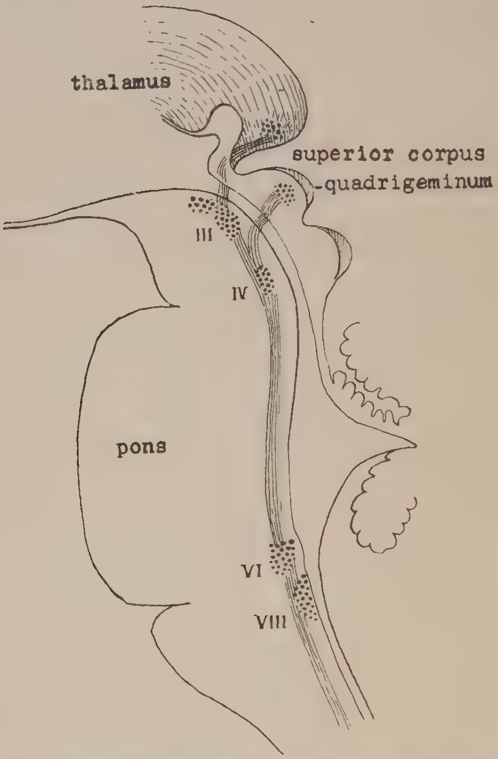


Figure 16.—Simple diagram to show the posterior longitudinal bundle and the nuclei of certain cranial nerves.

marshalled for producing the movements which are appropriate responses for definite visual impressions (see Figure 16). When the light comes to the surface and passing through the media already become transparent in anticipation, reacts upon the sensitive cells of the retina and so becomes translated to the sensory cells of the brain, the motor cells are ready to hand on the message and produce the appropriate movements of the eye. It would even seem that the workings of neurobiotaxis were not ended in the making of the human brain stem. The process may still be initiating alterations in the arrangement of the nuclei. In some cases of brain stem paralysis in which the nucleus of the hypoglossal nerve, which innervates the muscles of the tongue, is involved there is some impairment in the movement of the muscles of the lips. The lips, being part of the mechanism of facial expression, are innervated by the motor seventh, or facial nerve and therefore should be spared in hypoglossal paralysis. But although the lips may express emotion as part of the general play of the musculature of the face, they have thrown in their lot with the tongue in subserving the typically human activity of speech. It is not improbable, therefore, that in us the hypoglossal nucleus is tending to capture that part of the facial nucleus which innervates the lips and thereby create a neurobiotaxically grouped unit for performing the muscular movements for framing words. From the anatomical side this possibly latest human development of nerve cell grouping has not been verified.

CHAPTER VIII

LIMITATIONS AND THE RELEVANT STIMULUS

We have seen that by an underlying cytocletic action, which was termed neurobiotaxis by Ariens Kappers, the sensory nerve cells and the motor nerve cells become appropriately grouped and appropriately linked in the brain stem. We have seen how an incoming stimulus has everything prepared for it, even before its advent; and how this stimulus is passed on to the motor nerve cells and so is translated into appropriate action. We have learned how nerve cells within the nervous system may become linked by innumerable bonds, those bonds being expressed as the various anatomical structures known as dendrons, neuraxons, nerves, fibres, tracts, commissures, or white matter. The brain has become an organ of high complexity with ganglionic, grey nerve cell masses, devoted to the reception and to the handing on of stimuli, and grouped for producing appropriate response (see Figure 17). The brain cell masses are grouped for action and linked with each other and with other ganglionic masses of the spinal cord by fibrous, white, cell processes. The multiplication of nerve centres and the complexity of linkages can be carried on to bewilderment. It is as new exchanges and new connections can be added to the telephone system of a growing city: they can be added to till every house in the city is linked with exchanges and every district has its own exchange. But though a nervous system, built upon the lines we have been picturing, can far outdo any urban telephone system for complexity, it has its limitations in functional utility. Built as it has been built so far, it lacks something essential for progress. It is designed for the proper transaction of business between incoming sensation and resulting movement, it is designed to produce the most appropriate response to the stimulus.

It does not immediately admit of a choice of response. The incoming sensory stimulus is not examined, criticized, considered and then acted upon: it is acted upon at once by the production of an ordained, appropriate, life-saving response. By the wonderful underlying principle of cytoclesis the thing has grown so perfect as to become automatic; it is, to use a much abused term, reflex. The stimulus comes, the result is inevitable. The response is produced. The response is fitting and proper and, maybe, exceedingly complex: it may have every appearance of being the outcome of consideration and deliberation on the part of the animal, and yet it is all arranged for by the grouping and connection of the aggregations of nerve cells within the brain and spinal cord. The sensory stimulus comes, the appropriate motor response results: the response is necessarily apt, for it is determined on a life-saving principle, but its aptness must not deceive us into thinking it anything other than reflex. Its very appropriateness, and its inevitable appropriateness, are, in themselves, suspicious. It is not left to the animal to make a mistake by affording it the opportunity of varying the response.

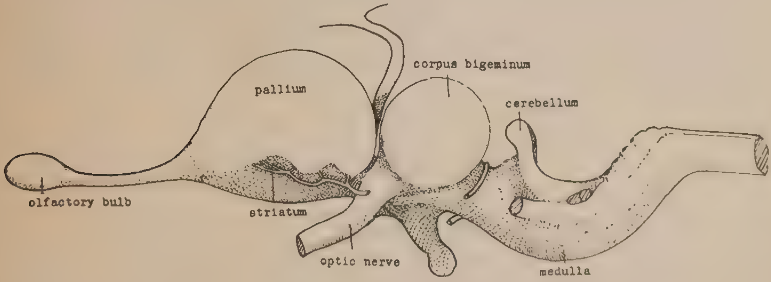


Figure 17.—The brain of a lizard (*Trachysaurus rugosus*) seen from the left side.

A nipple placed in a pup's mouth produces, as a response, the movements of suckling. An irritation of the skin over the region of its ribs produces, as a response, the movements of scratching with the hind leg. But these things though complicated are automatic; there is no choice left to the pup, else when the nipple came to the lips it might wrongly elect to scratch its side and, thereby, fail to suckle. There is no choice left to the animal; the appropriate response will be forthcoming and the animal's life be saved.

But if there be no advance upon this ground plan of the nervous system, there can be no advance in the direction of perfecting or varying the response. It is well not to give the young animal the chance to make a mistake; but it is not well to withhold from the mature animal the opportunity to improve, to vary, and to adjust the response. An animal that reacts to a stimulus by producing the most fitting response by virtue of the neurobiotaxically grouped nuclei in its central nervous system does not remember its response, does not gain experience by repeating the response, and does not become more perfect in effecting the response. The stimulus comes in, it produces its results and then, so to speak, is gone. It has fired a train, it will fire the same train every time, but nothing apparently is left behind in the animal. The animal is not capable of acquiring memories of feeling and movement, it does not correlate any particular sensory impression with other impressions or other movements: it does not vary or improve or make its reponse more suitable; it does not remember, it does not learn by experience.

The stimulus is needed every time, and every time the same response will be produced, no better and no worse for its repeated performance. Some stimulus will make, let us say, a fish snap with its jaws, and every time the stimulus is repeated the jaws will snap. It will not snap with increasing perfection as the process is repeated, nor will this particular snap be evoked in the absence of the stimulus. The fish will not snap in anticipation or in memory of the stimulus, it will not rehearse the act in the absence of the stimulus and thereby improve its aptitude in snapping. It will produce the appropriate snap whenever the proper stimulus is forthcoming. The stimulus may be the impression of an object moving through the water. It may be evoked by the presence of another fish upon which the species normally preys, it may be called forth by a manufactured imitation of a fish, or by an elaborate artificial fly, or a silver spoon or a mere tag of red flannel or a piece of an old sock. Anything that produces the impression which creates the stimulus will evoke the response. Even a fish may have its eye dragged out by a hook at which it has snapped, and almost immediately be hooked by snapping at its own eye impaled upon the hook. It would seem, then, that a definite stimulus (here that of an object moving through the water) produced a definite, though often complicated, response: that experience had little or nothing to do with the matter, and that the animal did not remember, or correlate its impressions and responses. It seems that the animal did not benefit by or harmonize the stimuli received by various channels, nor associate them with the varied (and appropriate) motor responses effected. So much seems obvious both from anatomical investigation and from the study of animal behaviour.

But there is a converse to this dictum. We have seen that a stimulus is needed every time in order to produce a response; that the response cannot be begot from what we will term the memories of impressions already received and appreciated. Since the response is, as we have seen, an appropriate, life-saving one that is specially adapted to the preservation of the individual—what of the stimulus? Will all stimuli reaching the central nervous system through the sensory channels evoke this response? Will trivial as well as vitally important stimuli call forth a life-saving response? Were one to be the arbiter of animal behaviour, one would certainly say No. We cannot permit every possible stimulus which comes from the outside environment of the animal to evoke a response; some stimuli must obviously be far too unimportant to the animal to warrant the production of an appropriate life-saving response. Were all stimuli to be judged and weighed by the animal, and the response left to its discretion, as an outcome of its experience and memory, then we could conceive the possibility of permitting all stimuli to affect it. But if only appropriate and biologically important responses are to be produced, then only life-saving and biologically important stimuli should be permitted to evoke them. This may be termed *the doctrine of the biologically relevant stimulus*: the stimulus which is necessary to produce appropriate response in the neurobiotaxically grouped nervous system.

We may say that the eye is a sense organ adapted for receiving and passing on the stimuli produced by rays of light. An animal that possesses an eye, possesses an organ sensitive to light rays and capable of passing on stimuli produced by these rays. We know that ether-borne waves with a wave length of somewhere between 400 and 800 millimicrons are capable of affecting the retina, but it does not follow that illuminated scenes and objects will affect the animal or be "seen" by it. The animal with no more than the neurobiotaxically grouped brain will "see" only that which is biologically important to it. If we take, for example, a goldfish living in a glass bowl set upon a table in the drawing-room, we may for the moment disregard the problems of the relative refractions of glass and air and water, and we must admit that a wide range of visual stimuli is always available to the retina of the goldfish. Yet how many of the visible things which have place in that drawing-room are seen, as we would use the word in regard to ourselves, by the goldfish? An ant's egg or a bread-crumb, falling through the water, may convey an impression from the retina to the brain and so produce a fitting response. But beside the occasional passing of an ant's egg or a crumb what a host of other sights are open to the goldfish in the drawing-room. To us these sights may be interesting or they may not; nevertheless, we see them and they enter into our consciousness in varying degree. But to the goldfish they are entirely unimportant: they are not biologically relevant stimuli, and they do not produce any effect upon the nervous system of the goldfish. The goldfish sees only a few of the sights contained within the drawing-room because only a few are of biological importance to it. Because a goldfish sees so little in the drawing-room, by reason of the smallness of its range of biologically relevant stimuli, it has never occurred to anyone to stigmatize the animal as being blind. But other creatures, not so commonly studied at close quarters, have been popularly regarded as suffering from defective vision, whereas they, in reality, suffer from defective visual appreciation. The common English Blind Worm (*Anguis fragilis*) may be taken as an example.

This limbless lizard is commonly regarded by country folk as being unable to see, since its behaviour shows that many of those visual stimuli which, falling upon our retina produce visual impressions and evoke responses, leave it entirely unmoved. Blind Worms behave as though they were blind in the presence of many visual stimuli which excite the retina and the nervous system of a human being. A Blind Worm might well have the whole drama of human life and death enacted to admiration within its sphere of vision and yet, this not being of much importance and, therefore, not a biologically relevant stimulus, it would remain unseen. *Anguis fragilis* may be completely blind to the immediate and unrestricted view of the most beautiful woman any tipsy poet has pictured, yet the least glimpse of the little putty-coloured, slimy slug, known as *Limax agrestis*, sets its whole organization amoving. I have had specimens of *Anguis fragilis* in captivity for over seven years and have had them at all stages of their life cycle. I have often wondered at the bright eye and the great appearance of visual intelligence and marvelled the more at the relative "blindness" of the creature. But the visual acuity is there to perfection.

There are few biologically relevant stimuli for *Anguis fragilis*; but let anyone who wishes to test its powers of vision (as distinct from its range of visual appreciation) arrange that a little grey slug shall wander into the picture and note the instantaneous effect that this produces on the Blind Worm. The little grey slug is a biologically relevant stimulus, since in the ordinary way *Limax agrestis* forms the elected article of diet of *Anguis fragilis*.

The biologically relevant visual stimuli for the Blind Worm seem to be few; but I have also learned that the relevant auditory stimuli are not numerous, and that *Anguis fragilis* might, almost with justice, have been classed among those animals, such as adders, toads, etc., which are popularly termed "deaf."

None of the customary noises of a busy laboratory seem to affect *Anguis fragilis* in the least; intentional efforts at producing a wide range of sounds meet with little better success. The creature does not hear them. They are of no importance and have no meaning to the animal. But let the tap drip, or allow water to drop from the rose of a watering-can, or arrange for an open window as the first few drops of a shower fall, and all is activity with the Blind Worm. Time and again I have watched this. Much bustle and noise may be abroad and all is unnoticed; but a gentle pit-a-pat of the first drops of water, so soft that one can scarce hear it, and the Blind Worm hears and acts upon the knowledge. Rain-drops, with their subtle little sounds of falling upon the turf, constitute a biologically relevant auditory stimulus for *Anguis fragilis* though a recital on the violin may leave it unmoved. And, again, the explanation lies in the vital importance of the stimulus. The drops of rain tell the Blind Worm that the little grey slug will be abroad. The pit-a-pat is the dinner bell and that is a sound all animals can hear. With a very large number of amphibians and reptiles which inhabit the more arid parts of Australia, the sound of rain-drops is a potent auditory stimulus, not because rain heralds the advent of the slugs, but because rain showers may be so few and far between that to miss one may be to miss all. It is all important that the sound of rain should be heard, and appreciated by animals living in semi-arid regions.

The sound of rain-drops affects *Anguis fragalis* in England and in the same way affects *Trachysaurus rugosus* or *Tympanocrypta lineata* in Australia; but a far better demonstration of the biologically relevant stimulus is available to anyone who cares to observe that common Australian frog, *Lymnodynastes dorsalis*. Take a *Lymnodynastes* and play the violin to it, sing to it, shout to it, make any vocal sound that can readily be produced—and the animal takes no heed. It is deaf to all these sounds. Keep it in the laboratory or in your private room and it takes no heed of sounds produced around it. The organ and the violin leave it unmoved, they are not biologically relevant stimuli; but I possess a specimen of *Lymnodynastes*—which incidentally has five legs—upon which I can produce an instantaneous and inevitable result by striking a loose tile on the floor with my heel. The sound produced by striking this loose tile resembles, in some measure, the croak of the frog and as certainly as the tile is struck so surely will the frog respond. Though I may laugh and shout in my room the frog is deaf to the sounds, but as I go from the room and in going step on the loose tile, though the sound produced may be very slight, yet it will be enough for the frog to straighten its fore-limbs and sit up and then inflate its throat and produce an answering croak. The imitation croak or the real croak all frogs can hear. They have also another biologically relevant stimulus, and this is the sound of a body falling into water. Should a pebble be dropped into a pool frogs upon the bank will clearly show that the sound is appreciated, for upon the sound they too will jump into the water. When one frog seeks safety by jumping into the pool it is time for others to do the same, and the sound of a splash is a biologically relevant—it may be a life-saving—stimulus for those frogs that pass most of their time in the water.

It is to be doubted if observers of animal behaviour and writers on animal psychology have always taken into consideration the paramount importance of recognizing the biologically relevant stimulus. Obviously we may be misled if we seek reactions from animals by producing stimuli that are not biologically relevant. Obviously too we may make false deductions if we only consider the structural perfection of the sense organ and neglect to study the functional attainments of the central nervous system. Psychologists have elaborated a method of deducing discrimination by reference to sense organ structure: the argument being that if an animal possesses a sense organ built upon similar lines to those present in our own sense organs, it is likely to be able to experience sensations or to be able to discriminate stimuli in a manner comparable to what we can conceive as the results of our own experience.

Curiously enough the only source of error in this line of argument which has appealed to the student of animal behaviour seems to be centred in the adequate functioning of the sense organ. "For clearly the mere presence of a sense organ bearing sufficient likeness to our own to admit of conjecturing its function could be of no value as proof unless it were shown that the sense organ actually functions" (Washburn). In this argument the whole responsibility is thrown upon the sense organ and no account is taken of the brain. It is not a question of the functional perfection of the sense organ: it is the functional perfection of the brain that is involved. He would be a bold man who examining the eye of a Blind Worm would predict that the animal could see a slug but would be blind to the flower upon which it crawls. Obviously it is useless to test the reactions of a frog by producing musical notes as auditory stimuli.

CHAPTER IX

THE RISE OF THE PALLIUM

Hitherto we have considered a nervous system built up on a very definite plan and capable of a very definite range of function. The plan has ever been the same, for the insunken surface cells have been sensory and motor in nature, they have received and handed on stimuli. They have received stimuli from the sensitized parts and handed them on to the acting parts. Moreover, by virtue of the phenomenon of neurobiotaxis, they have become so grouped that, from any given source, the stimuli are passed on to the motor cells which are connected with the muscles that will produce the most appropriate response. An appropriate response is produced and a relevant stimulus is needed. But we have noticed in all this a lack. The animal is equipped for dealing with the immediate demands of its normal routine of life, but it is obvious that the routine must needs be a somewhat restricted one. Its life may be said to consist in the performance of appropriate actions begot in response to biologically relevant stimuli. The animal does not manifest its activities in the performance of ever-varying responses to ever-varying conditions. It does not lead a life of lights and shades of response; it does not exercise that deliberated choice of action such as is manifested by animals more advanced in the evolutionary scale.

There is necessarily a lack of variety in the neural activities of those animals whose brains have not advanced beyond the stage of development marked by the precise adjustment of motor and sensory ganglionic masses. They are well fitted to do as their forbears did: they can do as did their whole phylogenetic line and make appropriate responses to relevant stimuli. They are well equipped for dealing with the usual and the essential: and in the presence of the usual and essential the response is perfect. A Blind Worm may react as the whole phylogenetic line of Blind Worms has reacted. It is as though its neural channels were well-worn pathways along which the relevant stimulus makes easy passage and finds its outlet in the perfection of adequate response.

It is, however, not well that an animal should always, and only, be prepared to deal with the usual; nor is it well that an individual should be inevitably limited in its neural activities to that repertoire that has been rehearsed by its whole long line of ancestry. If progress is to be made, it is necessary that the unusual as well as the usual may receive proper response from the animal. It is necessary that the individual should, as an individual, be able to react to stimuli and adjust itself to circumstances that have not been encountered and responded to by its forbears. There is a demand for something more in the way of neural activity: there is developed something more in the way of neural architecture. A new element is begot and this new element may be said to consist in an aggregation of specialized intercalated cells; cells so to speak interposed in the circuit between the sensory and motor cells of the ganglionic masses of the brain. There have already been ordered nervous centres in the brain: there have been co-ordinating and controlling mechanisms: there has been developed all the perfection of neural grouping by the agency of neurobiotaxis: but the new cell area is something in addition to all this. Stimuli may enter the more primitive brain and flow easily through the accustomed channels begot by neurobiotaxis; they may find their outflow in the production of appropriate action. There is no place for overflow. The usual produces its wanted response: there is little structural differentiation for dealing with the unusual. It is in the new intercalated cells that we may look to find place for the overflow: and that overflow evidently comes from the stimuli derived from the world around the animal. It is in connection with the receptive ganglia of the exteroceptive sense organs that the intercalated cells first take their rise. In the lowest vertebrates the field occupied by these new cells is insignificant, in the reptiles it is considerably larger: but in its perfection it is the possession of the mammals. It is that part of the brain that has permitted those great cerebral advances which, definitely initiated in the lower vertebrates, rise suddenly to higher complexity in the mammals and culminate in man.

In the brain of the lower vertebrates, so far as we have considered it, we have noted a complex mass of nerve cell aggregations grouped in appropriate linkage and arranged so that easy paths are laid down for the receipt and discharge of relevant stimuli and adequate response. Such a brain is a rather solid affair consisting of cell masses, gathered into various anatomical forms, and constituting what is known as the basal ganglia or central grey matter. The new element, the added cell field, is not developed in the midst of the basal ganglia; it becomes the pioneer of a new anatomical entity that takes the form of thin, hollow, bilateral outgrowths from the brain stem (see Figure 18). These outgrowths develop from the older co-ordinating masses of the brain stem and over them they spread as a mantle. This is the beginning of the *pallium*. Though all forms of terminology are open to criticism and the use of the word pallium has been so much debated as to have a literature all to itself, we will not discuss these things. For us the pallium will be the whole of the new mantle element that constitutes the two primitive *cerebral hemispheres*. These cerebral hemispheres form a comparatively trivial portion of the brain in the fishes and amphibians: they are well established in the reptiles and become the dominant parts of the brain in all mammals. In the cerebral hemispheres are the new intercalated cells that constitute the grey matter and their issuing and communicating neuraxons that compose the white matter: the pallium is therefore a complex mass of neurons and neuraxons and their intercommunications. Since the pallium grows out as two hollow spheres which, in the perfection of their human development, tend to cover up the whole of the brain stem, we may regard it as being, in such case, the outside of the brain as opposed to the basal ganglia which constitute the inside of the brain. It is this human condition that has given rise to the most generally employed terminology. For the old anatomists the brain, like many other organs of the body, consisted in a central part comparable to the pulp of an orange and a covering layer comparable to the rind. The central part was termed the *medulla* and the rind the *cortex*. The central part consists of the basal ganglia and the masses of neuraxons, and part of this medulla is prolonged from the brain and to the spinal cord as the *medulla* *prolongata* or *medulla dorsalis*. It was not until 1754 that the appropriate name of *medulla prolongata* was changed by Archangelus Piccolominus to the now familiar *medulla oblongata*. The rind of the orange is the mantle of the brain, and so that which we are terming pallium will be practically that which is known as cerebral cortex, when in

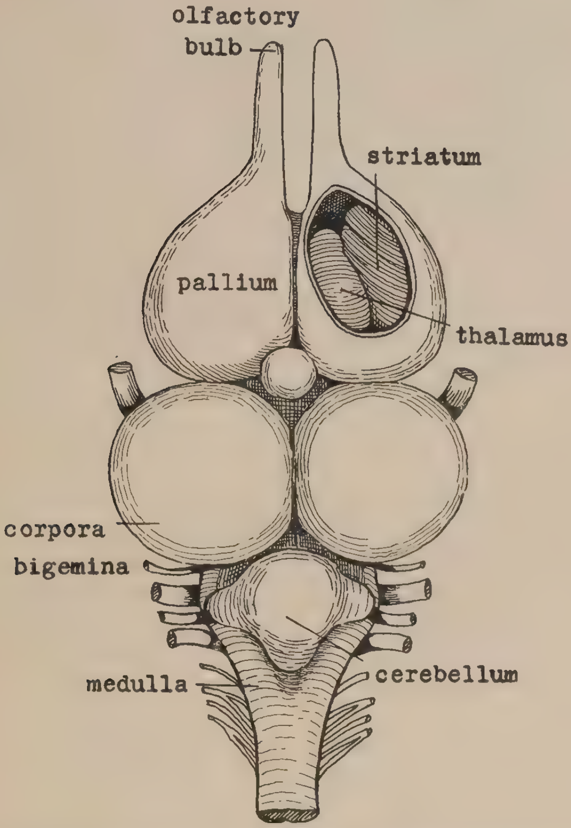


FIGURE 18.—Purely diagrammatic representation of the essential parts of an idealized primitive vertebrate type of brain. The upper surface of the brain is figured and the roof of the right cerebral hemisphere has been cut away.

the term cortex we include both the cortical grey matter of the intercalated cells and the cortical white matter of their associated neuraxons. We need not press definition to extremes, the more so when we realize the vast bulk of neurological literature that deals solely with the attempt at precision of terminology and neglects the broader issues of the function of the parts defined. For our purpose the term pallium will include all those parts of the mantle of the brain that grow out from the brain stem as the cerebral hemispheres, and by cerebral cortex we shall understand those layers of pallial intercalated cells which constitute the surface strata of the hemispheres. This is the structure that enlarges the range of life possibilities for the animal: this is the organ into which we picture neural overflow to take place, which permits of the unusual as well as the usual being responded to and this, not by a stereotyped though adequate response, but by varied and individual reactions.

If we confine our attention to the function of vision we may perhaps get some idea of the change that the presence of the mantle has produced in the animal. All ether-borne waves of one short octave, which we know as light, can affect the sensitive cells of our retina; and we can only assume that this octave affects the retinae of other animals. But of all the objects illuminated by such rays, there are, as we have seen, only a few which may affect the Blind Worm's retina. We may say that such an animal does not appreciate or react to the whole series of stimuli which light is capable of producing on its retina. We may say that the eye as a sense organ has its sensory receptor cells in the brain stem unconnected or insufficiently connected with pallial cells.

Add the pallial cells to the sensory basal brain cells which subserve the function of vision and then appreciation of all visual stimuli will come. A wide range of objects, relevant and irrelevant alike, will be seen and reacted to though all will not produce a motor response.

We can appreciate the difference between an animal that has no pallium for vision and one that possesses a pallium to which visual stimuli find their way by watching a human patient recovering from damage to his cortical area for sight. We can appreciate the difference also by watching animals in various stages of the development of a visual pallium.

But we may, in the case of vision, note the difference in an altogether different way. The brain that sees only the biologically relevant stimulus is a brain not greatly, nor constantly, employed with visual stimuli. Impressions only stream to it and affect it at maybe infrequent intervals. But a brain that sees everything and reacts to all pictures cast upon the retina, is one much and constantly employed so long as there is light enough to permit of vision.

Here is a difference; in the one case a brain that is only rarely called upon to deal with stimuli caused by rays of light: in the other a brain that is open to the reception of all stimuli caused by light so long as light persists. It may be said that in the first case there will be no likelihood of the production of visual fatigue. There will be little chance that the brain will be kept on the alert by visual stimuli. But with the addition of a visual pallium it is different, and in order to rest the pallium from the fatigue of the instreaming impressions, there must be some method of cutting off the light stimuli from the retina. This is the birth of the eyelids. Though it is often asserted, and more often imagined, that eyelids are developed in order to protect the eyes of animals that live on land emancipated from the water, this is in reality only half the truth. It is true that fishes have no eyelids and that men have: but we must not forget that all snakes and many lizards, though living wholly on land, possess no eyelids. We may therefore get an idea of the rise of the pallium in which vision is represented by noting the development of the eyelids (see Figure 19). A snake we would suppose had only the neurobiotaxically grouped sensory and motor cells subserving vision; and we would expect it to react only to biologically relevant stimuli. A crocodile we would expect to have the third element in the brain and to possess some pallial cells devoted to vision; we would also expect it to appreciate a wide range of visual stimuli: a range so wide that when it would sleep, and cut its brain off from stimuli, it must close its eyes in order to obtain pallial rest. A man may see more things with his eyes shut than a snake may see with his open: and this for the reason that man has a portion of his pallium allotted to visual impressions. But it is not only with vision that the pallium is concerned, and

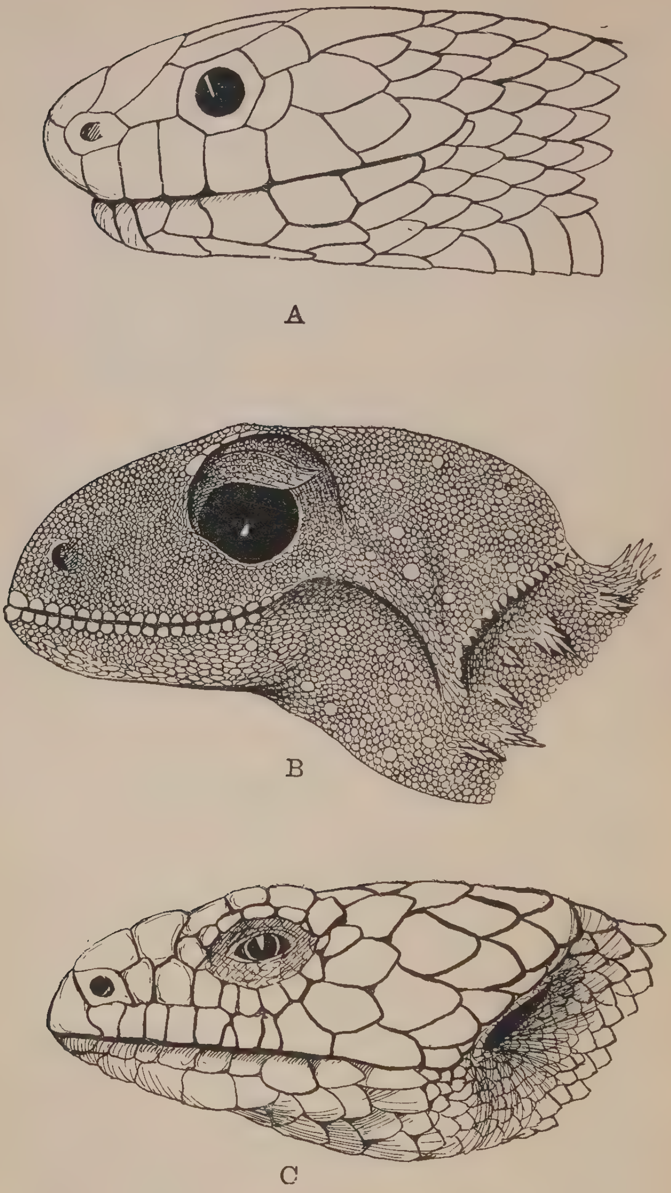


Figure 19.—The heads of three Australian reptiles. A, a snake (*Denisonia coronoides*); B, a gecko (*Nephrurus asper*); and C, a lizard (*Trachysaurus rugosus*), to show stages in the development of eyelids.

vision, as a function of snakes and men, has only been cited for the purpose of a simple illustration. The pallium in its perfection is concerned with all things, it becomes the mechanism for dealing with impressions gathered by every sensory channel, it becomes the neural centre for all those sensations that can possibly affect a complex animal.

The pallium we may therefore regard as being a structure added to the old brain stem and one that rises somewhat suddenly to importance in the mammals. We may assume it to be the organ that is developed in order to permit the animal as an individual, and not merely as the child of a definite line of ancestry, to deal with the varied stimuli that may affect it as an individual. We have seen that the stimuli that demand the development of the pallium are those that arise from the environment and are received by the exteroceptive sense organs. But just as the exteroceptive stimuli demand a new field of neural connections and find it in the cerebral cortex, so, as we shall see later, the proprioceptive stimuli demand their new co-ordinating mechanism and they find it in the development of another cortex—the cortex of the cerebellum.

CHAPTER X

SURFACE AND VOLUME

Since the pallium is to become the dominant part of the vertebrate brain and is to be the triumph of all nervous organization there must be ample provision for its anatomical growth. It must be a thing capable of enlargement without producing any upset in the evolutionary trend of the developing animal form. It is to grow as a mantle, as a hollow enveloping mass, enshrouding the basal nuclear portion of the brain, and in continuity with the sensory and motor nerve cells of the neurobiotaxically grouped brain to which it is added. But all the while that we are wondering at the marvels of the mantle, we must not forget the axiomatic fact that it is made from an inturned portion of the surface of the body. It is necessary to keep this constantly in mind, for in this remarkable origin lies the solution to some of the curious circumstances that befall the pallium in its development. We might suppose that the amount of inturned surface would bear some relation to the amount of surface left exposed. Since the inturned surface, or central nervous system, has to interpret the messages transmitted by the outer exposed surface, we might reasonably assume that an animal possessing a large exposed surface would have a large central nervous system, a large brain, and, when the mantle has arisen, a large pallium. We would therefore suppose that, other things being equal, the size of the brain of an animal would be dependent upon the size of the animal. A big animal would have a large brain simply because its body is large and its external nervous system is therefore extensive.

But in all this we must remember that it is the surface that counts. It is the surface that is sensitized to the stimuli coming from the outer world; it is the surface that demands an extensive inturning of cells to constitute the nervous system which is to receive these stimuli and which is to act on them. It is the surface of the animal that matters: it is not the mass or weight or volume of the creature that is of importance. We may say that the larger the animal is the larger its brain will be, and this is a general truth, but there are one or two details to be considered before we can dispose of the question. As an animal increases in size, its growth of surface does not keep pace with its growth in volume. An animal that has ten times the volume of another animal does not possess ten times its surface area. That *volume outruns surface* in enlargement of more or less spherical figures is a thing to be remembered: for obviously it is useless to employ mere bulk as the criterion of comparison between the sizes of animals and their brains. We must not compare the weight or the bulk of animals, we must compare their surface areas in order to get an idea as to the proportionate sizes of their brains. This being so, it is easy to see that with rapidly increasing bulk there is only slowly increasing surface area and only slowly increasing brain stem and pallium. From the standpoint of general adjustment to its environment, it will, therefore, never pay an animal form to become gigantic. Though a gigantic animal may have an extraordinary large brain, its brain will be small relatively to the bulk of its body, since the creature's sensory skin surface is small relatively to the mass of its purely vegetative parts.

A whale possesses an enormous brain: a brain that weighs over ten pounds (4,700 grams). It possesses the largest brain of any living creature. But the whale possesses a gigantic body. Its body weighs something like 25,000 times as much as its brain, and so it is that, though absolutely its brain is the largest found in any living animal, relatively to its vast bulk of body it has the smallest brain of any living mammal. A whale has a large surface and it, therefore, has a large brain; but the animal is so large that its surface is relatively small in comparison with its huge bulk, and it, therefore, happens that relatively to its enormous body it has a ridiculously small brain.

In the porpoise, a smaller animal akin to the whale, the brain, though absolutely far smaller than that of the whale, is relatively far larger. A whale's brain may represent 1/25,000 of its body weight, whereas, in the porpoise it may reach the very high proportion of 1/38. It does not pay to make animals gigantic. Obviously their bulk is likely to outrun their pallium. Indeed, though we state this as though it were a fact that we had discovered on behalf of Nature, such has been Nature's own experience. Gigantic animals are no longer made, and such as persist into our day are rapidly passing away.

In speaking of the rise of the pallium we have said, that, "other things being equal," the size of the brain of an animal is dependent upon the size of the animal. In this phrase "other things being equal" has been inserted of a definite purpose. We may legitimately compare the brain of a porpoise with that of whale. Both animals belong to the Order *Cetacea*, both animals are living in the present epoch. More than this, both animals are aquatic creatures, without any sense of smell, and with a completely naked body surface. The fact that they have no sense of smell leads to an atrophy of the parts of the brain connected with this sense: the fact that their bodies are naked implies a

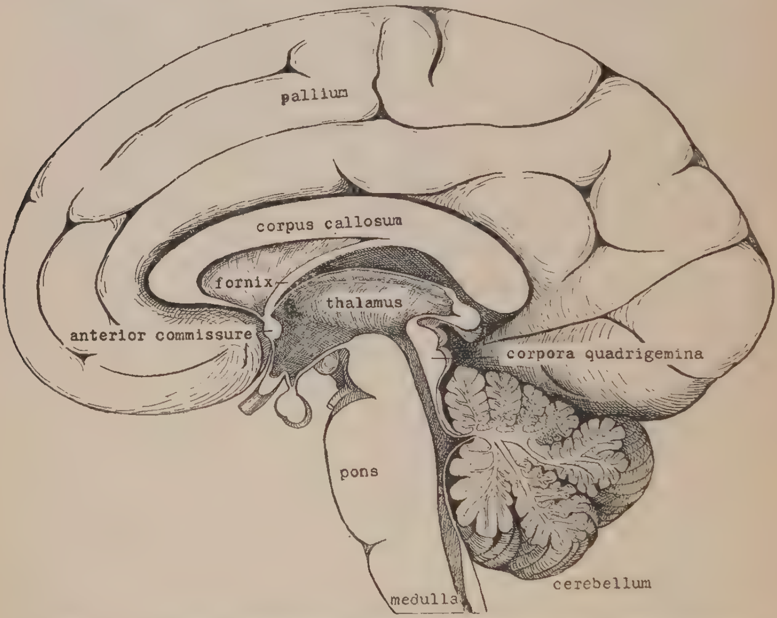


FIGURE 20.—The right half of a human brain which has been divided in the middle line.

surface sensitiveness which is naturally all-important in producing cerebral (pallial) advance. But we must not press comparisons too far—we must bear in mind that phrase "other things being equal." Surface of body, as mere surface, needs further examination before it can be taken as a criterion of brain size. Not only the area of the exposed surface, but the quality of the exposed surface must be considered. The surface is of importance as the sensitive, knowing, learning area. But surfaces will differ in this respect: some animal surfaces may be highly sensitive, some relatively insensitive. In one case there will be more to tell the brain from a small sensitive surface than there may be from a large comparatively insensitive surface in another case. It may not seem well to face the world with a very sensitive and, therefore, unprotected exterior. It may seem a gain in animal structure to protect the animal by armour plate of some kind or other. Armour plate protects an animal. Armour plate deprives the surface of the animal of sensitiveness, deprives the surface of its right to demand a large inturning as the brain.

We know that volume tends to outrun surface. We realize that if the surface of the body be kept naked and sensitive as in the porpoise and the whale, the large whale will in the end be handicapped by its vast bulk and its relatively small brain. But suppose that, instead of a naked sensitive surface, Nature has decided to introduce some armour plating. The end is easy to see. Gigantic animals, even with sensitive exteriors, are inevitably failures. Animals that are armour-plated and deprived of sensitive exteriors are inevitably failures even though they are not gigantic. A gigantic armoured animal is inconceivable as a success—and indeed Nature has long since found this when she dispensed with the large armoured animals which so much attract the visitors to the palaeontological galleries of our museums. Armour-plate and large size marked Nature's ambitions when the age of Reptiles was at its height. Sensitive exteriors and comparatively small, active bodies marked the Mammals whose day was to come when that of the Reptiles was done. But even the early Mammals possessed brains that were extremely small when comparison is made with those of their modern representatives. Great brained Man we must own is, in addition to all his other assets, not a little lucky in being a middle-sized and an entirely naked animal.

Now the fact that volume outruns surface not only dominates the relation of pallial growth to body size, it determines certain characters of the pallium itself. We have agreed to accept the nomenclature of the old anatomists who regarded the brain as consisting mainly of two parts, the cortex or rind and the medulla or kernel. The rind is the surface portion of the brain and the medulla is the volume of the brain. The surface is the all-important pallium; the volume is, in the main, the nerve fibre masses coming to and going from the cells of the pallium. Now it follows that, as the brain increases in size, the pallium will lag behind relatively to the central fibre mass. Owing to this inexorable law of surface and volume we may make the general statement that a small animal will have a small brain because it is a small animal, but that, since the animal's sensory surface is large in proportion to its vegetative bulk, its brain will be relatively large. Now this absolutely small, but comparatively large, brain, will have a surface which is large in proportion to its volume. We may, therefore, say that a small animal is likely to have a brain which is relatively large and one which possesses a pallium which is of ample proportions with regard to the white or nerve fibre mass of the medulla. This is the condition of the small, sensitive type of alert animal representative of several mammalian Orders. But it is obvious that as the animal grows larger and its brain consequently increases in size, there must be some effort made to keep proportion between the growth of the medulla and the growth of the pallium. The pallium is so all-important that some steps must be made in order to attempt to keep harmony between the increase of surface and the increase of volume in the enlarging brain. The solution of the problem is a simple one. Let the surface be puckered and thrown into creases and folds and so extend its area; and then the folded surface may increase proportionately with the central portions of the brain. Folding of the pallium into sulci and gyri is a mechanical means for overcoming the lag behind of the surface growth with the geometrical increase of volume. Gyri and sulci—the convolutions and fissures of the brain—have been almost worshipped by some people as indications of intellectual advance: but we need to be cautious before we make assertions as to the "intelligence" of any animal when intelligence is estimated from the convolutions of its cerebral cortex. The convolutions may mean nothing more than that the brain is absolutely a large one and so its surface must be folded in order to keep pace in growth with its central parts.

A little animal with an absolutely small, but relatively large, brain has a brain which, since it is small, has a surface large in proportion to its volume. In such an animal there is no need for the pallium to wrinkle or fold. Such an animal may have a perfectly smooth brain and yet have a very high proportion of cortex or pallium to brain mass and a very high proportion of brain to body mass. As a matter of fact Owen's Lissencephala, or smooth-brained animals, are simply the small Mammals; and it is now well recognized that the small members of any Order have smooth brains simply because they are small. Complete absence of folding of the pallium so that convolutions and fissures are not present in any form is therefore no indication that an animal will be unintelligent—if the animal be small. On the contrary a smooth unconvoluted brain, if it be present in a small Mammal, is likely to be a guarantee of a very efficient pallial representation and control.

For those who worship convolutions regardless of all the circumstances of their formation, the brain of a whale provides a splendid object lesson. The brain of the whale is not only the largest brain, but it is also the most highly convoluted brain. This high degree of convolution is merely the outcome of its great growth and the expression of the desire to keep surface growth in harmony with volume growth: it is no indication of intelligence.

The highly convoluted brain of the whale represents, as we have seen, about 1/25,000 of its body weight. There are small Mammals in which the brain is relatively a thousand times larger than is the case with the whale, and in them the cortex or pallium is innocent of any convolutions. The inflexible demands of a law of geometrical proportions, the simple relations between surface and volume must, therefore, not be overlooked in our enthusiasm to estimate the rank of an animal by its cerebral convolutions.

CHAPTER XI

STRUCTURE AND FOLDING

It is nearly a century ago that the fact that a brain becomes convoluted because it grows larger was first made clear from the study of a series of mammalian brains. It was in 1845 that Dr. Baillarger, one time alienist in the Asylum of Charenton in France, gave a clear statement of the general principles involved. The original expression of the facts in Baillarger's words is as follows: "La différence entre le rapport des volumes et des surfaces est le résultat d'une loi mathématique: que les volumes des corps semblables sont entre eux comme les cubes de leurs diamètres, tandis que leurs surfaces sont entre elles comme le carré de ces diamètres, ce qui donne des proportions très différentes. Le cerveau subit cette loi à laquelle il est cependant soustrait en partie par l'existence des circonvolutions."

To-day his principle is accepted in neurology and passes under the title of *Baillarger's Law*.

Baillarger understood why the mantle of the brain puckered. The puckering is in itself no indication of intelligence or of high status in the animal scale: it is simply the natural result of growth. A very little study, however, makes it clear that, though the folding of the pallium results from obedience to a simple physical law, it produces no mere haphazard wrinkling of the surface. The pallium does not fold at random in order to increase its area. The folding occurs at more or less definite places, and so a basal pattern of gyri and sulci is characteristic of the brain of any species of mammal. There is a well-known underlying ground pattern for the gyri and sulci of the human brain. Individuals may show a wide range of variation in the details of the pattern, but, nevertheless, the ground plan, which is common to all human brains, is there. The folds perforce must be formed but it is obvious that some factor determines the site of their ordered formation. What is the factor? It might be sought in outside influences. It has been supposed that the formation of sulci is due to the presence of blood-vessels on the surface. It has been said that the more highly developed and the more complex a brain became, the more complex its vascular supply had to be and so the surface of the pallium became more elaborately sculptured into hills and valleys by the presence of the vascular channels. The vascular causation of the surface pattern of the human cerebral hemispheres has had a wide, but a vain, advocacy extending down to within thirty years of the present day. Again, it has been supposed that the necessity for packing a soft and enlarging brain within a rigid skull cavity determined the formation and the site of the sulci and gyri. It is impossible to deny that the shape of the skull and the shape of the brain must be related: but it is not conceivable that the hampering influence of the retaining skull can determine the precise localization of each furrow. The fissures are formed when the brain by no means packs the cranial cavity; they are even formed if the skull remains, in great part, undeveloped. Although a recent attempt (1916) has been made to revive the doctrine of skull pressure, it is fair to say that no success had been met with, and that the thesis may be regarded merely as a literary curiosity. More reasonably it has been suggested that the main direction in which the growth and enlargement of the pallial outgrowth occurs has some influence in determining the general disposition of the foldings. Doubtless there is some truth in this, but not for the simple mechanical reason that the brain is squeezed and puckered as a mass of dough would be.

If then outside influences do not seem to offer a likely cause for the production of orderliness in pallial puckering, we may look for some inside influence, some peculiarity in the pallium itself. Baillarger knew why the pallium had to fold ; strangely enough it was he who also gave the true solution of the problem embraced in the orderliness of the site of folding.

On February 2nd, 1776, Gennari when studying the structure of the mysterious cortex of the brain saw in the grey surface layer of a certain region of the hemisphere, that "linola albidior admodum eleganter" which now we know as the line or *stria of Gennari* (see Figures 21 and 54). Gennari's line is a pale stripe which subdivides the grey surface layer of one portion of the cortex into two strata: from the surface inwards we may easily recognize, with the naked eye, a grey layer, a white layer and then a deeper grey layer. It was Gennari who first realized that the grey pallium was no simple rind, but was itself a complex layer. After an interval of sixteen years Vicq D'Azyr, unaware of the previous work of Gennari, redescribed this white streak in the grey cortex and impressed upon a wider circle of disciples the fact that the grey cortex was a composite of layers which could be seen by the unaided eye. Parchappe subsequently recognized two layers in the grey matter, Cazauvieilh described three, and these three were said to be everywhere present in the cortex. In 1840 Baillarger communicated to the Royal Academy of Medicine the results of his examination of the structure of the cortex. In his classical paper—"Recherches sur la structure de la couche corticale des circonvolutions du cerveau"—he described six alternate strata in the building up of the grey matter, and he noted that in different parts of the brain the layers were very differently disposed.

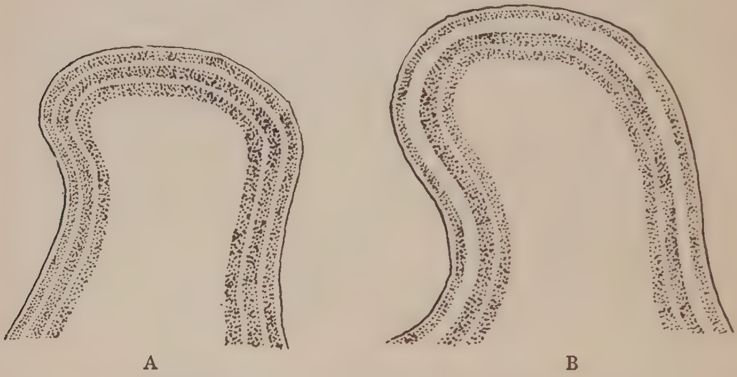


FIGURE 21.—Baillarger's determination of cortical structure. A shows the six typical layers of the cortex. B is the section of a convolution showing the stria of Gennari—the broad white third layer.

Gennari had described one line which justly bears his name; but in 1840 it became obvious that Gennari's line was only one of a series of what are now universally known as *Baillarger's lines*.

Now here we have three separate facts. In animals with large brains the pallium must fold. The pallium is complex in structure and moreover the structure varies widely in different areas.

We have seen that it is obvious that the pallium does not fold at random as its increase in area takes place, else would all brains show different patterns of sulci and gyri.

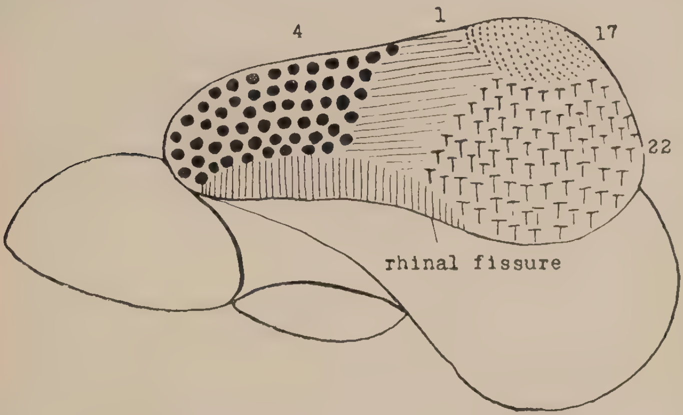


FIGURE 22.—The histological topography of the cerebral cortex of a terrestrial insectivore, *Macroscelides* (after Elliot Smith). In this figure and in figures 23, 24, 25 and 26 the rhinencephalon is represented white and the pallial areas are distinguished by the conventional signs introduced by Brodmann. Parts of the pallium primarily connected with movement 4: sensation 1: vision 17: hearing 22.

Is it then the varying structure of different areas of the pallium that determines the site of the wrinklings?

When the pallium has to fold in order to maintain its necessary growth ratio, does it fold at predestined sites determined by the varying nature of cortical structure? Here is a question upon which much study has been expended and much ink outpoured.

It would be an easy thing to imagine that a surface layer which had of necessity to fold, would wrinkle at places where the structure became weaker or less resistant. We might expect to find sulci related to definite changes in structure of the layers of the cortex. But although this is a reasonable expectation all observers have not been agreed as to its actual fulfilment. We may say that in this matter there have been two schools. The men of one school were absorbed with minutiae: they were much concerned with securing a high degree of accuracy in their observations and looking for a corresponding precision on the part of nature. Many distinguished German neurologists were of this school. The men of the other school, though not unmindful of the scientific demands of accuracy, had no great desire to impose upon nature the rigid adherence to precision which they were prepared to accept as a standard in their own doings. Many English anatomists were of this school.

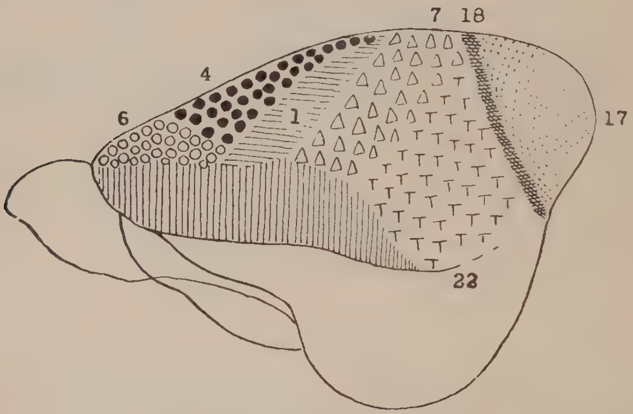


Figure 23.—The histological topography of the cerebral cortex of the Pen-tailed Tree Shrew, *Ptilocercus* (after Le Gros Clark).

There are two methods of studying cortical structure and its relation to the formation of sulci and gyri. We may take small portions of the cortex and study their structure, much magnified, under the microscope. The structure is magnified, moreover the areas in which structure changes are magnified. Since transitional areas between two types of cortical structure are magnified, the transition from one type of structure to the other seems a gradual thing, taking place over a wide area. In this way the school of the microscopists has, for the most part, conceived that areas of different cortical structure are graded insensibly into each other over a wide intermediate area; and that this wide intermediate area bears no very sharp or precise relation to a cortical fold. But the other method of investigating the question produces rather different impressions. We may attack the problem by studying the naked-eye appearance of the cortex of perfectly fresh brains. In this method the whole brain is sliced and the characters of the cortex noted. Here we will see Baillarger's lines and the different cortical structure fields marked off sharply from one another. The large intermediate area has vanished under naked-eye inspection, one field joins another at a sharp boundary—and, moreover, this junction has a definite relation to the pattern of sulci and gyri of the surface. Which school is in the right? Which method ensures a proper understanding of the problem? In 1913 an exhaustive summary was made by Ariens Kappers of the contentions of the two schools; and as a result of his labours it was made evident that the right lay with those who were content to see nature working to homely approximations and disregarding the niceties imposed by the high powers of the modern microscope. That fissuration of the pallium follows, in the main, the lines of cortical structure is now established beyond all doubt.

To some it may seem strange that the rather more homely worker, using his naked eye in preference to carrying out elaborate histological investigation, should arrive at the truth concerning the boundaries of cortical structure and fissuration. To some it may seem to be reactionary. Surely the man with the high-power microscope and precise methods must see more accurately. That may be; yet he may not see more clearly. To some it may have happened that for long they have walked about a familiar country-side. It may be the surroundings of the village of our boyhood. We knew all the features of the surroundings as the man with the high-power microscope knows the structure of the cortex. We walked in a region of familiar gradations because we saw all so intimately and so minutely. To some it may have happened that, since the day of walking those familiar scenes, they have regarded photographs taken from aeroplanes including the area of their once minute perambulations. Here is the naked eye view. Here are the sudden boundaries, the sharp changes, the map-like arrangement, unguessed at as we saw all at near range. In truth we may wander round our village in intimacy, as the microscopist wanders among the fields of the cortex, and never note where the squire's land ends and the glebe begins. But the bird's-eye view from the aeroplane, in the one case, and the naked eye view in the other gives us a sharpness of outline and a reality of contour never guessed at in the more intimate methods of study. It is not necessary to adhere to any mere mechanical conception of the relation of cortical structure to cortical folding to agree that the two factors are related. Indeed it is little likely that it is the difference in physical surface texture that brings about the observed relationship. It is the fact that folding of the surface is the necessary method of increasing the surface and that certain structural fields need special increase in area that is nearer the root of the matter.

Now this is a great thing. We are agreed that cortical folding, in the main, follows lines of cortical structure. We have seen that Baillarger realized that the cortex varied in structure in different localities. Since Baillarger's time, vast strides have been made and now we have come to recognize that there are upwards of forty different fields of cortical structure. The pallium of grey matter is, therefore, a mantle in which there is a great variety of structure. Different fields vary in their texture and different fields tend to be delimited by surface foldings easy to distinguish.

At this stage we may pause to take stock, for we are upon the threshold of something far more widely reaching. We have followed Baillarger in concluding that the enlarging pallium must fold. We have followed him in recognizing that the structure of the grey cortex is not uniform all over the pallium, we have followed, what may be called the English School, in agreeing that pallial folding follows lines of pallial structure. We have yet to apply the great maxim of John Hunter that "Structure is only the intimate expression of function."

CHAPTER XII

STRUCTURE AND FUNCTION

Owing to the route by which we have travelled we stand in no need to defend or to define the doctrine of the cortical localization of function. We have seen that the pallium is an addition to the brain. We realize that it is added to a brain in which different sensations and different movements have their station, or are represented, in ganglionic masses arranged by the dictates of neurobiotaxis. The various sensory impressions are already represented in the basal grey masses, they will become rerepresented, in the pallial grey matter. We should, therefore, expect the pallium to be portioned out among the senses: we should expect to find that function was localized in the pallium as it was in the basal grey masses. We should not expect the cerebral hemispheres to act as a whole as do, say, the lobes of the liver, even if function be not in them strictly pigeon-holed in minute and rigidly defined areas.

But though, from our method of approach, this is our expectation, we must remember that the doctrine of the cortical localization of function has had a slow emergence and a hard fight for acceptance.

In order to appreciate the reason for the apparently late acceptance of the doctrine, one must realize the circumstances under which it was first impressed upon the scientific world. Long before the opening days of the nineteenth century men had formulated opinions: but in the year 1800 Spurzheim, as he himself says, "attended for the first time the private course of lectures which Dr. Gall had been in the habit of delivering occasionally at his house for four years." After 1800 nothing that had gone before mattered much, so far as the question of cortical localization of function was concerned. In 1804 Spurzheim, having completed his studies, joined Gall and until 1813 the partnership continued. What that partnership produced all men know. Rather, all men know that of the partnership was begot the fabric of phrenology and all the odium attaching to its study. There are fewer who know that of it was begot the doctrine of cortical localization. Here was cortical localization carried to extremes; carried into dreamland and romance with a bewildering blend of precision and speculation more fitted to dreamland than to science. The orthodox scientific man was concerned to discount the claims of the phrenologists, and indeed in many directions he met with no very difficult task. But there is always a danger that in a massacre, even if only a massacre of doctrines, the innocent may suffer with the guilty. In the feverish efforts at the destruction of the creed of phrenology, the teaching of cortical localization was destined to suffer.

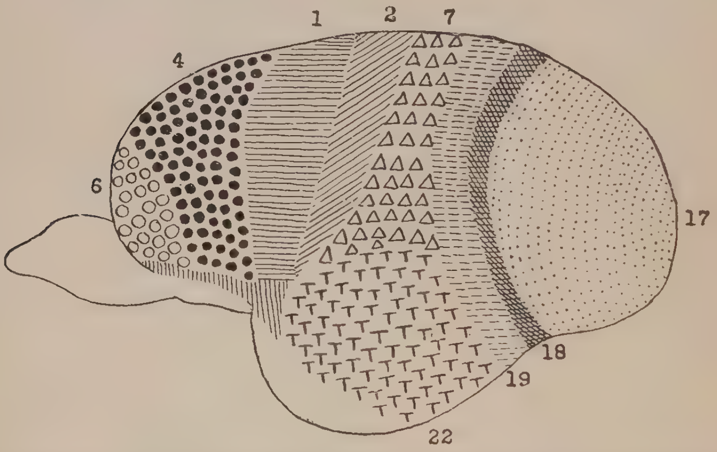


FIGURE 24.—The histological topography of the cerebral cortex of the most primitive of the Monkeys, *Tarsius* (modified from Wollard and Elliot Smith).

Fleurens disproved the one thesis as easily as he did the other. In demonstrating that the cerebellum showed, when investigated by scientific methods, no signs of being the centre for sexual love, it was easy to go a stage further and declare that the brain acted as a whole—that there was no such thing as cortical localization of function. The credulity of the phrenologists in this strangely complex period of neurological thought is only less marvellous than the incredulity of the orthodox scientist. Certainly we may say, in looking back on the period, that the orthodox school vastly underrated the minute and intimate knowledge of the brain possessed by Gall and Spurzheim. Probably we may say that another century will have to pass before these men receive due credit for their real additions to knowledge. Not till the odium of the follies of phrenology is forgotten will Gall take his place among neurologists. Morgan's model busts must all be broken up and lost for ever before our attitude alters: and if this should seem an exaggerated statement, we have only to turn to the modern text-book approval of the experiment in which Fleurens destroyed the "cerebral hemispheres" of pigeons in order to disprove Gall's contentions. In dealing with the human cortex Gall was postulating pallial functions, in removing the cerebral hemispheres of a pigeon Fleurens was dealing with the very type of brain most difficult for us to understand, since it is essentially a non-pallial brain. Fleurens' experiment, though quoted with present day text-book approval, had no bearing upon the question of the function of the higher mammalian pallium. Moreover, it was made on rather dangerous ground for no one who has any acquaintance with the works of Gall and Spurzheim can admit that the comparative anatomy of the brain was one of their weak points. Equally fallacious were the arguments brought against Gall's doctrines that the cortical gyri represented foldings of a substance that was not structurally nor functionally identical in the whole of its area. Lewes in his *History of Philosophy* propounded an argument that carried great weight with the opponents of Gall's teachings. He said: "The convolutions of the brain which Gall has mapped out into several distinct compartments, each compartment being the organ of a distinct faculty, are in reality not more distinct than several folds of a piece of velvet; and a little more reflection discloses the absurdity of supposing that one portion of this velvet could be endowed with different properties from every other portion, simply by virtue of its superficial position. The tissue of which the convolutions consist is the same throughout its folds." Lewes was far from the truth in this, his strongest

LINACRE COLLEGE LIBRARY
UNIVERSITY OF OXFORD

argument against the claims of the phrenologists, but he was justified to the extent that he was writing at the very time when Professor Ecker was lamenting that anatomists represented the convolutions of the brain "much as they would a dishful of maccaroni."

So much of advocacy is not an apology for phrenology, it is a plea that the phrenologists be forgiven their phrenology and admitted as the true pioneers of the doctrine of the cortical localization of functions. Whatever we may determine to do now or in the future, it cannot be denied that the acceptance of the doctrine was delayed by at least half a century simply because it was the doctrine of the phrenologists.

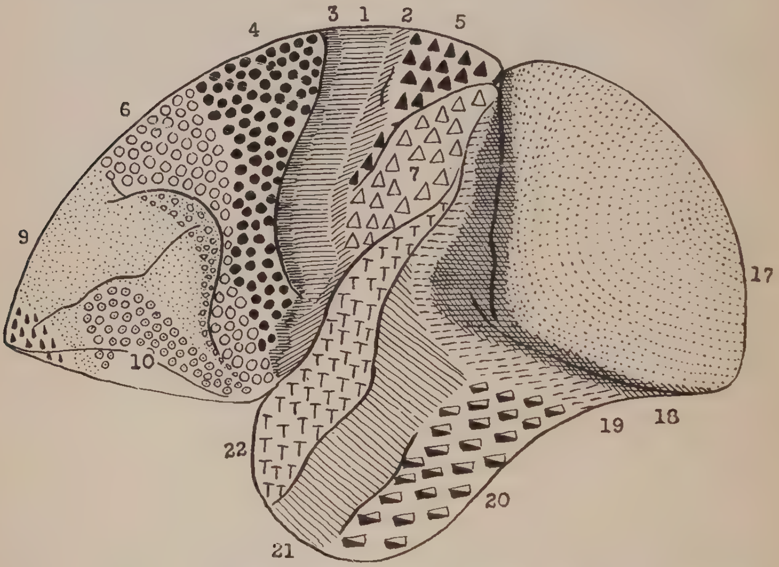


Figure 25.—The histological topography of the cerebral cortex of an old-world Monkey, *Macacus* (after Brodmann).

When the storm period was over (Gall died 1828) the accomplished Frenchman, Paul Broca, called the attention of the scientific world to an instance of what appeared to be a demonstration of the reality of cortical localization. This announcement was made in 1861 and it concerned that portion of the human pallium now known as *Broca's convolution.*

In 1864 Dr. Hughlings Jackson, working at the bedside of patients in the London Hospital, demonstrated in the clearest manner the two great facts that the cortex was excitable and that function was localized in it. There are those who would do away with eponymous nomenclature, but we should be the poorer by a great deal were Broca's convolution and *Jacksonian epilepsy* to pass for ever under other names. Broca noted the cortical defect that was present in two persons who had lost the power of framing the vocal symbols of language: he determined the cortical site of the motor centre for initiating the muscular movements of speech, by noting the site of the damage in persons who had suffered from aphasia.

Hughlings Jackson noted the start and progress of Jacksonian fits and correlated his observations with the results of the operations undertaken for the relief of the patients, or with the anatomical findings revealed at autopsies. He determined the cortical site of the motor centres for various parts of the body and limbs in persons in whom some irritation had stimulated the cortex and produced twitchings and movements of the parts.

Now followed the experimental school, and cortical localization received attention from an army of eager men who placed the whole doctrine on a sound basis. But though we must admire and give due place to those, the best minds among the physiologists, who carried out the endless series of experiments on animals, we must not ignore the clinicians. Too much importance is apt to be given to what is called research, when by that term is meant work carried out in the seclusion and detachment of a laboratory—too little appreciation is at times given to the work done by observant medical men at the bedsides of their patients. The experimental physiologist has played a great part in determining the details of cortical localization; but the clinician must always hold the trump card. Though we experiment on apes, it must be remembered that animals cannot tell their experiences, and their actions may thereby prove misleading. Pathological processes in one way or another are always performing experiments upon human beings, and these victims of experiments can tell the clinician of their experience and so prevent the drawing of possibly incorrect deductions. It was thus that Broca learned and thus with Hughlings Jackson. It was pathological processes, making experiment with humanity, that gave Dr. Alfred Campbell the material upon which he placed cortical localization upon a newer and a firmer basis. Campbell's work was published in 1905 under the title *Histological Studies on the Localization of Cerebral Function.* In this great work the structure of the normal and diseased human cortex was determined and a new line of attack was carried out. Hughlings Jackson had noted movements in a limb when the cortical area was irritated. Broca noted the area of the brain damaged when a patient could not perform a definite act. Campbell studied the cortex in patients who had suffered, during life, the loss of some part. If the cortical area determined by Hughlings Jackson as being allotted to the movements of the leg be correct, we would expect to find some alteration in that area in a person whose leg had been amputated early in life. This was the work that Campbell did: and thereby carried the doctrine a stage further.

Experiments on animals have probably taught all that they are capable of teaching us concerning cortical localization. In 1914 the inquiry again passed from the experimental physiologist to the clinician.

Between 1914 and 1918 military projectiles performed more experiments on human beings than all the carefully designed operations carried out on animals by the experimental physiologists.

The research of 1914–18 was not carried out in the seclusion of laboratories; nevertheless it is the research which has given us our greatest increment of knowledge concerning the human brain. We may say to-day, with some claim to accuracy, that the human brain has yielded many of its secrets and among them the details of the localization of function in the different areas of the pallium.

We may now make a synthesis of results. We have seen that repeated laborious investigations of cortical cytology have established the fact that pallial folding follows lines of pallial structure. We have seen that pallial function, like pallial structure, is localized to definite areas of the brain. Campbell, twenty years ago, brought out the truth of the Hunterian maxim that structure is the expression of function and that pallial structure and pallial function are correlated. The vast experience of the European war has confirmed the experimental evidence, accumulated during the last half-century. We are thus brought to a satisfactory conclusion. We are agreed that the pattern of the human cerebral cortex, constituted by the sulci and gyri, is in the main a pattern made in accord with cortical structure, since the foldings of the pallium are an expression of pallial cytology. But pallial structure, we have seen, is the outcome of pallial function and we, therefore, arrive at the interesting and important conclusion that the pattern of the cortex of the brain is a rough chart of cortical localization of function. This finding gives to the main gyri and sulci a very real value. As Morgan's model busts presumed to give the areas mapped out by the phrenologists, so do the gyri and sulci of the actual brain delimit the areas in which definite functions are localized. In the one case an extraordinary and misplaced zeal determined some thirty-eight areas on the outside of the head; in the other, patient investigations into

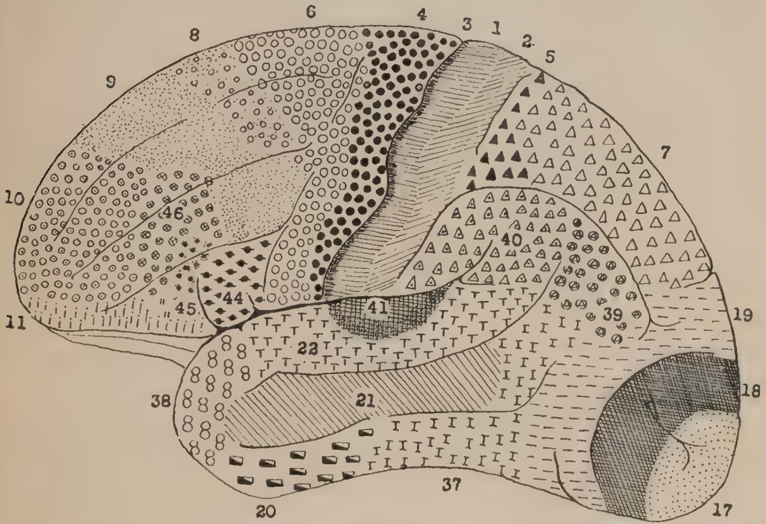


FIGURE 26.—The histological topography of the human cerebral cortex. The figure has been compounded from the results of several investigators.

cortical structure have determined some forty areas on the pallium (see Figure 26). In the one case "bumps" on the skull are the guides to the areas, in the other the gyri and sulci on the cortex of the brain constitute the boundaries. There is always a danger that when a thesis long suspect is at last accepted as orthodox, its acceptance may be somewhat undiscriminating. Doubtless this process has played its part in the doctrine of cortical localization: there have been those who had delight in allotting each separate element of psychic activity to a very circumscribed cortical field much in the way that the phrenologists located their "faculties" in rigidly defined areas. The process of confinement of cortical functions within narrow pallial limits has probably gone too far in some directions and we must steer a middle course between regarding any given function as being discharged by the cortex as a whole and picturing the cortex as a mosaic of rigidly delimited functional areas.

CHAPTER XIII

ORDER IN REPRESENTATION

When once the developing brain has attained the structural and functional complexity expressed in the rise of the pallium it may be said to have set up a council table for stimuli at which all its senses will demand a seat. But there must be an order in which the seats are allotted and the order must be maintained as the council table enlarges and the councillors become more numerous.

Here, again, we are thrust back upon the very simple state of affairs comprised in the circumstance that an animal which possesses bilateral symmetry moves through the world with one end constantly directed forwards. This advancing end, as we have seen, is destined to be the informative end, its sense organs will be the informing special sense organs, its receptive ganglia will be the brain. This is the just claim of the advancing end, that it is the pioneer in all things concerned with brain building. It will, therefore, be most fitting that the most advanced sense organ, the one which first meets and knows of outside things, shall be the councillor to take first seat at the table. This first councillor is the sense organ of the first cranial nerve—the great olfactory guiding sense. It is olfactory stimuli which first demand admittance, and are first admitted to the pallium; the first pallium is an almost exclusively olfactory pallium. From the inception of the pallium in its primary olfactory phase it is possible to follow its rise to perfection through that series of animals which we have every reason to believe constitutes our phylum. But we must remember that by the possession of our brains and sense organs we are able to appreciate the reactions and sensations of other animals having brains and sense organs constituted upon similar lines to our own. We must not go too far with this business. The whole arrangement of the nervous system of the invertebrate differs from that of the vertebrate; invertebrates possess sense organs undreamed of among the vertebrates. He is, therefore, a hardy fellow, being a vertebrate, who would read into the doings of an ant the sensations which affect him, the judgments which sway him, or the impulses which determine his conduct. This hardihood is not uncommon, but here we will have none of it and from all our speculations we will exclude invertebrates. With the vertebrates we are on safer ground, for we too are vertebrates, but, even with them, we cannot proceed far in our study of pallial development without realizing our limitations. I understand what is meant when we speak of olfactory sensations, or the sensations carried from my nasal sense organ to my brain by way of the first cranial nerve. I have a right to assume that I can adjudicate upon these sensations in animals with nasal sense organs much like mine and living, as I do, in the air. But I cannot lightly assume that I understand what sense is subserved by the first cranial nerve sense organ of a fish living in the water; especially when I realize that olfactory sense organs of the type which I possess atrophy when a mammal takes to an aquatic life. Again I cannot pretend to know if the term "olfactory" sense applies in any measure whatsoever to birds. The mammalian sense of smell is obviously a different thing from first nerve sensibility as it is manifested in fishes; and once this first nerve sensibility has become evolved into an appreciation of air-borne chemical stimuli received upon a definite olfactory placode, it is unable to revert to its previous primitive condition. It shows to perfection the working of the *Law of the Irreversibility of Evolution*: a primitive aquatic first nerve sense may evolve into an air-borne olfactory sense, but when a mammal reverts to a purely aquatic life its olfactory sense cannot retrace its evolutionary steps and its only course is to atrophy. It may be that the primitive vertebrate first nerve sense is more akin to taste than to smell and if we cannot precisely define its particular rôle in the functional complex of the special sense organs we at least know that its great importance is in the sampling of objects that may or may not be desirable as food. Nor can we adjudicate upon the actual sensations that are received by the organ of

Jacobson—part nasal, part buccal in its anatomical situation, possibly part olfactory, part gustatory in its functional rôle. Jacobson's organ appears first in certain fishes, it is present in amphibia; and in mammals it would seem to be related to the business of food-getting in such forms as retain it in functional perfection. In man it is a mere rudiment and we are quite unable to appreciate what actual quality of sensation it may minister to in other mammals. In the marsupials it is large in the pouch-embryo and in mammals generally its functional rôle would seem to be related to food-getting in the dark. We may therefore postulate that whatever the type of sense organ the first cranial nerve may supply it is essentially concerned with those stimuli which are useful to the animal in its quest for food. Nor must we forget that the primitive thalamo-striate complex from which the pallium grows is in itself a mechanism mainly devoted to the stimuli and the movements involved in the business of food-getting.

Within limits we may claim to be able to appreciate the stimuli that affect a primitive reptile, within limits we may claim to understand the reactions of such an animal, for the generalized reptile brain presents a fair picture of the beginnings of our own brain.

But with birds we may take no such liberties: the avian brain is of a structure so different from our own that to read our cerebral processes into the doings of birds is an extremely risky business. We are, therefore, concerned with no forms save mammals, for of their sensations and reactions we may alone make judgment with any degree of safety.

With lowly mammals it is a matter of the simplest observation to appreciate the degree to which they are guided by olfactory impressions. Scent rules their lives, they are slaves to their nasal sense organs. It is not that their eyes or ears or other sense organs are not used. They are used just as they have always been used throughout the whole story of the animal series: but the stimuli streaming in through them do not obtain so large a share of representation in the pallium. We may say, crudely, that other stimuli stream in and, if important, produce a response and then are gone: but olfactory stimuli stream in and, gaining the pallium, are raised to a higher neural plane.

A mammal that is a slave to olfactory stimuli noses its way through life. Everything met with is tested by the olfactory sense organ and the animal's experiences and memories are mainly those derived from the, to us, nebulous world of scents. But the very act of nosing its way about the world leads to another highly important result. The olfactory sense organ is situated right at the front end of the animal, and since it is the warning sense it is carried well in advance of the moving animal. In other words the creature has an elongated snout which goes before it through the world. Such a little animal may be pictured as being not very unlike an insectivorous Shrew or a Marsupial Pouched Mouse, animals which, though definitely sundered by basal anatomical features, are strikingly alike in general external characters. These little animals not only possess elongated snouts, but the ends of their noses are naked, and the snout is abundantly provided with vibrissae in the form of the familiar whiskers. The naked area of the rhinarium we will examine later, noting here no more than that it is a sensitive area. The vibrissae need further examination. The foremost bristles upon a primitive mammal's head are those represented along the margins of the upper jaw. These are known as the mystical vibrissae; behind them are the supraorbital, genal, submental and interramal groups of sensory facial bristles. The mechanism of these hairs is that their free tips extend some way in advance of the animal, and that their roots are in connection with branches of the great sensory nerve of the face, the fifth cranial, or trigeminal nerve. They are highly sensitive outliers of the advancing head end of the animal, triggers to fire a response the moment their free tips make contact with outside objects. It is these hairs, which are perpetually bombarding the sensory ganglia of the brain with stimuli as the animal noses its way through the world, that next demand a seat at the council table. Sensory impressions from the facial vibrissae next demand pallial rerepresentation in the mammal.

Although we may not turn aside to inquire what actual quality of sensation claims pallial rerepresentation from the snout and face, we may, even at this stage, substitute the term "awareness" for "sensation" and say that after the olfactory stimuli have gained pallial rerepresentation the next thing to be added to the pallium is the awareness of the snout and face.

A great addition is now made to the animal's stock-in-trade of pallial impressions, associations and memories. It has a realization of the muzzle region and of its movements and contacts and it may correlate this realization with olfactory impressions and be aware of the harmonized attributes of an object which has a definite spatial relation to its tactile snout and which also possesses a definite odour.

Here we may leave the primitive mammal to its terrestrial activities, living its life upon the ground to which trails of scent will cling, following its friends, avoiding its foes by olfactory impressions and learning of outside objects mainly by the correlation of tactile and olfactory sensations. What its fate may be does not concern us for the present; we are not immediately interested in the animals that cling fourfooted to the earth. The pioneers of our phylum became arboreal, they emancipated themselves from the thraldom of scent, they placed themselves in a position in which visual and auditory stimuli became of vastly greater importance, and they liberated the hand from the servile business of supporting the body weight in progression. There is no need to follow these things in detail: the playground of the branches in which the human infancy was passed, was a playground upon which was won the perfection of the human pallium and, therefore, of human intellectual and ethical distinctions. As we have seen, we have every reason to believe that the snout region was the first portion of the body to force its rerepresentations into the pallium. A cortical awareness of the snout, or a conscious knowledge of the position of the snout, became a pallial function, of the presence of which the sensory vibrissae of the muzzle and face serve to remind us. The snout is the examining area of the body, its vibrissae test novel objects and inform the animal and so demand a rerepresentation in the cortex. But in an animal that lives among the branches, the hand is saved from servile supporting functions and becomes the testing area of the body. Examinations of novel objects are carried out with the hand rather than with the muzzle and the hand demands pallial rerepresentation. The hand has this advantage over the muzzle as a sensitive testing member,—that testing by the hand is carried out under the inspection of the eyes. Visual stimuli now force their way into the pallium in ever-increasing streams and sight becomes more abundantly cortically rerepresented. The examining hand and the co-ordination of hand and eye between them lead to a wide knowledge of the animal's own body and soon cortical awareness of more than snout and head is added in an area of the growing pallium. Auditory stimuli, in the stock from which we spring, gain admission to the pallium, and now we have a completed mantle so far as functional rerepresentation is concerned (see Figure 27).

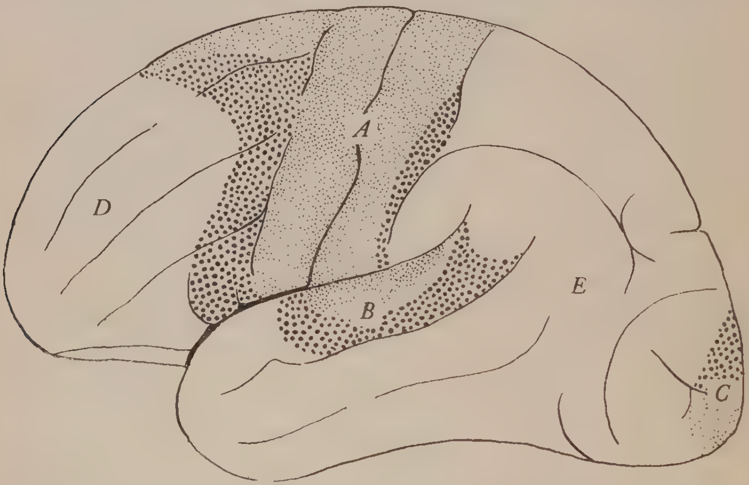


FIGURE 27.—The functional areas of the cortex of the human foetus as determined by Flechsig from the study of the development of the fibre tracts. A, Body projection area. B, Auditory projection area. C, Visual projection area. The fine dots in each case indicate the chief focus of the area. D, Frontal association field. E, Parietal and temporal association fields. Compare with Figure 26.

In carrying the outline of the story thus far it must be remembered that we have taken no account of the actual sites in the pallium where these different functions gain rerepresentation. We have paid no attention to the details of cortical localization, though we have assumed that there will be definite place for definite function.

Our mammal started with a pallium which was largely olfactory in function, and these new things streaming in by way of the thalamo-striate complex were added in the midst of this olfactory pallium. The older olfactory portion of the mantle becomes marked off by pallial foldings from the area dominated by the newly arrived stimuli. As the newly added stimuli demand increasing pallial areas, the old olfactory cortex becomes relatively diminished and, by the general method of the expansion of the mantle, is thrust mainly to the lower part of the cerebral hemisphere. Upon the upper and lateral surfaces of the pallium are the cortical areas for that quality which we have termed awareness of portions of the body (but which is usually labelled "motor and sensory" areas), for visual, and for auditory stimuli, in that order from front to back.

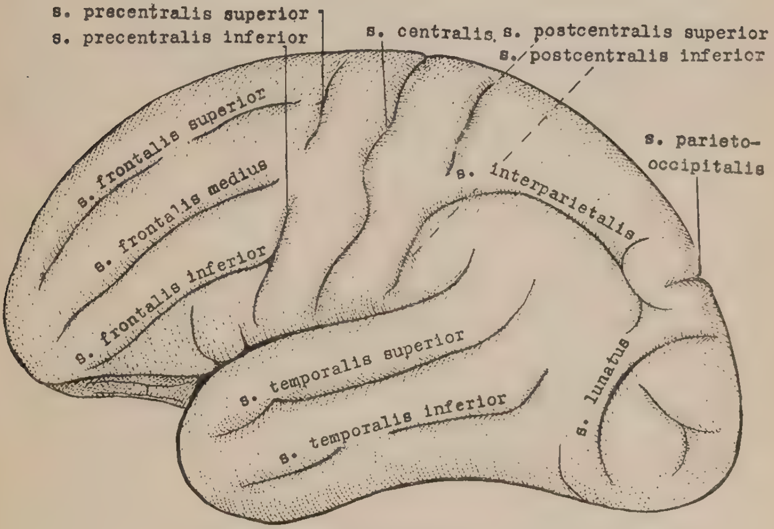

s. precentralis superior
s. precentralis inferior
s. centralis
s. postcentralis superior
s. postcentralis inferior
s. parieto-occipitalis
s. frontalis superior
s. frontalis medius
s. frontalis inferior
s. interparietalis
s. temporalis superior
s. temporalis inferior
s. lunatus

FIGURE 28.—Lateral surface of the left cerebral hemisphere showing only the essential elements of human cortical fissuration.

Smell (and taste) are therefore driven to the margins and below; movement, sensation, vision and hearing have localized cortical areas upon the lateral surface of the upper part of the cerebral hemisphere: and, from what we have already seen, we would expect, in animals which have convoluted brains, some surface indications of the extent of these areas.

One other thing must not be overlooked. The olfactory area is steadily diminishing, and being steadily thrust towards the margins of the hemispheres, and the great enlargement of the cerebral cortex, in the Primate series that culminates in Man, might be thought to be due entirely to the growth of the rerepresentation areas of movement, sensation, vision and hearing: but this is not so. As the final stages of pallial enlargement are accomplished, it is not the enlargement of the rerepresentation areas of senses that accounts for the growth. It is the development in between these areas of neutral zones, buffer states, or as they are termed in neurology, *association areas*, that accounts for the final stages of brain enlargement which distinguish Man from the lower animals.

CHAPTER XIV

THE RISE OF THE SMELL BRAIN

How all-absorbing are the stimuli derived by the first cranial nerve in lower mammals is a thing difficult or impossible for us to appreciate. It conveys but little to us to realize that the major portion of the cerebral cortex of a primitive Insectivore is given up solely to the dealing with the impressions of scent. We are more likely to be astonished at manifestations of the acuity of the olfactory sense than we are to marvel at a creature whose associations and memories are almost entirely bound up in scents pleasant or unpleasant. First in order of the sense organs, foremost outlier of the advancing end of the sensitive head of the animal and first to gain a place in the thalamo-striate complex, the olfactory sense is the master guiding stimulus in all lower mammals.

When mammals first arose and first adopted their characteristic covering of hair in some form or other, they exempted the most advanced portion of the moving body from the necessity of growing hair. Naked noses were permissible though it was necessary to clothe all the rest of the body with hair. Without going too far ahead in speculation we may say that mammals probably arose from a protoreptilian stock and became differentiated from that stock by reason of their greater bodily activity, expressed by, among other things, the carrying of the body clear of the ground. This greater bodily activity necessitated, and resulted from a more active metabolism. With this more active metabolism was the necessary accompaniment of a greater heat production by the physiological processes carried on in the laboratory of the body. This heat produced by the heightened metabolism must be conserved. If it is not conserved it will be lost, lost by radiation from the surface. The body heat we may say is created in the volume and radiated from the surface and again the business of the relation of surface to volume is intruded. Small animals will have large radiating surfaces when compared with their inner heat generating parts. Large animals have relatively less surface for heat loss and more for heat generation. There is much difference in this respect between an elephant and a mouse. The earliest mammals we have every reason to suppose were small creatures: their heightened heat production was therefore accompanied by a relatively large surface for heat loss. Hair as a non-conducting material met the requirements of the case, and the naked or scaled skin became clothed with hair. In the case of the evolving bird, feathers subserved the same function: but in the case of the birds the non-conducting feathers provided other possibilities beyond that of mere heat conservation. Hair was essential to the earliest small mammals, for the very reason that they were mammals and they were small. As mammals grew large they could afford to shed their hair, since their surfaces were relatively less in extent when compared with their volume. An elephant can afford to be hairless, but the hairless mouse outside the shelter of a nest is a curiosity.

Now though the little early mammals needed a hairy covering for the whole of their bodies, they did not impose the necessity for growing hair upon the most anterior part of the body. We are so accustomed to the presence of the naked nose, or rhinarium, in the mammals that it has ceased to be an object of curiosity. Not only is the rhinarium naked, but the skin that clothes it is usually of a peculiar texture. It is often tessellated, or granulated or patterned in some way or other and is of a peculiar fine, shiny, quality. Let those who have no more primitive mammals at their command examine the nose of an ordinary dog. In the early mammals a mechanism was introduced for moistening the surface of the eyes. We have already seen that eyelids were not developed because animals left the water and lived on land, but we may say that the lachrymal glands are present in order to keep the eye of the land-living animal moist. The moisture, which bathes the eye, escapes down the tear duct and so is carried into the cavity of the nose. The inside of the mammalian nose is kept moist, not only by its own secretion, but by reason of the tears that flow into it. It is a familiar thing that when a child cries it has to sniffle in order to prevent the tears running out of its nose. Normally our tears do not run out of our noses and the tips of our noses are therefore dry.

Our nostrils are completely ringed round. But if we examine the nose of a primitive mammal we shall see that the nostril is not a complete ring, for the margin is slit up at one side and a gap is left in the ring (see Figure 29).

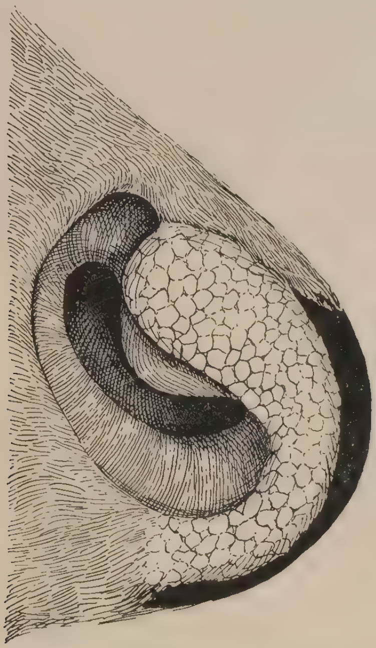


FIGURE 29.—The form of the nostril typical of those animals in which the sense of smell is highly important.

This gap is on the outer side of the nostril and it points along a line directed towards the inner angle of the eye. The line from the slit in the nostril to the inner angle of the eye marks the site of the tear duct; and this duct is formed by a meeting of skin over the line of its course. In an animal with a slit nostril, therefore, the tear duct is not so completely turned into the nasal chambers as it is in an animal whose nostril is completely ringed. In us, we must sniffle when we weep to prevent the tip of the nose becoming wet, but in the primitive mammal with the slit nostril the tip of the nose is always wet. The tears have served their turn by moistening the eye and washing foreign bodies from the sensitive translucent media, they have escaped by the tear duct and now fulfil a new rôle by moistening the tip of the naked mammalian rhinarium.

It may not be obvious to dry-nosed man what advantage there may be in having a rhinarium of which the naked skin is constantly moist. Yet the advantage is real enough.

When the wind is very light, so light that one can see nothing moving that will tell the direction whence it blows, old sailing ship sailors will moisten a finger by licking it and, holding it aloft, feel on its moistened surface the presence of what little wind there is. The moistened surface soon detects the presence of the moving air and appreciates from which direction it is moving.

A wet-nosed animal we would, therefore, expect to be an animal endowed with a high degree of olfactory sense and, moreover, one to which it was important that the direction whence the scent came should be realized. The wet-nosed animal might be the hunter or the hunted; to be efficient in either case a knowledge of whence comes the scent is essential.

The wet-nosed dog hunts by scent, the dry-nosed cat by sight. The wet-nosed dog follows its victim's trail, the dry-nosed cat stalks it. Wet-nosed cattle graze with their noses towards the wind and recognize danger and take alarm from scents borne on the wind. Dry-nosed horses graze with their tails to the wind and recognize danger and take alarm at sights or sounds which seem possibly hostile. It is for the man who pits his intelligence against that of beasts to understand these things. The wet-nosed animals are the aristocrats of the smell world. They must always be a little ahead of all the other animals, for to associate position, direction, and possibly distance with the receipt of a sensory stimulus is, as we shall see later, a very great gain indeed. We may, by sniffing to all points of the compass, find a direction of maximum intensity of a smell and so in the end localize it: but we all know how laborious this localizing process may be.

An animal with a wet, cleft nose has much more information at its disposal every time a scent stimulus is perceived upon the sensory olfactory mucous membrane. It has some idea as to the spatial relation of the scent.

But this is not the only advantage that the slit nostril possesses. At the site of the slit there is a cushion facing into the nostril and by means of muscles the cushion may be used as a stopper to the nostril, and so the animal may open and shut its nose. The play of the mobile nostril is very remarkable in wet-nosed animals and the least breath blown in the direction of a deer is enough to set the mechanism working.

So much simple observation teaches us of the great importance and the sensitive mechanism of the olfactory organ of lower mammals.

There are many other evidences. We may tell how important the sense of smell is by the fact that so many animals possess specialized glands for producing scent in order that their friends may follow them. Such glands as are intended to leave a trail are generally situated upon the lower surface of the body or even on the feet themselves and are evidently placed so that their secretion may come in contact with the herbage or with the ground. We may examine the complexity of the nasal chambers and see the wonderful arrangement of thin scroll-like bones covered with mucous membrane spread so as to catch the current of incoming air. We may look at the skull and observe the large and numerous holes through which the olfactory nerves pass to the nasal chambers to supply the mucous membrane. We may watch the behaviour of animals and even if we have not at our command a Shrew or a Pouched Mouse, we may yet learn a great deal from a dog. We have all seen a dog sniff under a door in order to find out if his master is in the room, or watched him sniff down a rabbit hole to learn if the tenant is within. And there are other curious things in the scent life of a dog not so easy to explain nor so nice to discuss: and, as one of the least unpleasant, we may mention the dog's method of putting scent on his handkerchief which consists of rubbing his shoulders into, and rolling upon, offal.

Perhaps the most striking demonstration of the discriminative sense of smell possessed by a dog is the well-known experiment carried out by Romanes. Romanes possessed a favourite setter which was accustomed to follow him in his walks and would pick up his scent in preference to that of others; but in his absence would follow the scent of the gamekeeper. The experiment consisted in forming a line of twelve men, at the head of this line Romanes marched and the gamekeeper brought up the rear. As they marched, each man stepped in the footprints of the man ahead. At the end of a march of two hundred yards Romanes turned off to the right and five of the others followed in his steps: the seventh man at the same point turned to the left and the remaining five men with the gamekeeper in the rear followed him. The two parties proceeded in opposite directions and then secreted themselves. When the setter was placed on the trail it followed the undivided track to the point of bifurcation, momentarily overran the parting of the ways, and then without hesitation followed the right-hand trail. The footprints of its master were overlaid by those of eleven other men and moreover the most recent impression was that of the gamekeeper, and yet the animal could evidently pick out and follow the trail left by Romanes.

Better even than experiment are the actual findings of anatomy: we may examine the brain of a lowly mammal and see the condition of the olfactory portion of the pallium.

Such a brain as that of the beautiful little marsupial known as *Dasycercus cristicauda* (see Figure 32), when looked at from the side, appears to be built up of two stories in the region of the pallium. The two pallial stories are separated by the groove of a sulcus, the sulcus being known as the *rhinal fissure*.

The lower story of the pallium or *pyriform lobe* is the old olfactory mantle, connected with the olfactory ganglionic masses in front; the upper story of the pallium is the non-olfactory mantle into which movement, sensation, sight and hearing are clamouring for rerepresentation. The groove that separates the two stories is a pallial fold formed at the junction of the two areas of different pallial structure. In this animal we may say that about half the pallium is elaborated in association with the olfactory apparatus and about half with the mechanisms subserving all other functions.

Dasycercus is a primitive marsupial; it is carnivorous, a scent hunter with the dimensions of a large mouse and the blood lust of a tiger (see Figure 30). It is active, predatory and crepuscular. It lives in a burrow of its own making, a master of the circumstances in which it finds itself, a perfectly adapted animal and one that has preserved a very large number of primitive mammalian characters, among them the large olfactory pallium.

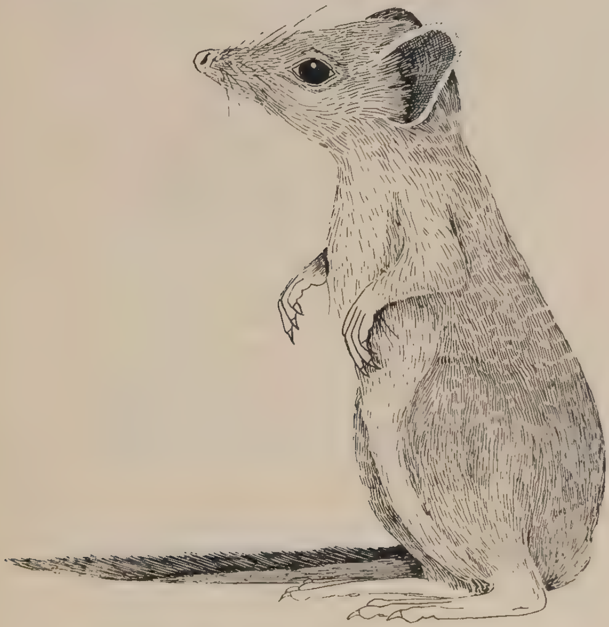


FIGURE 30.—*Dasycercus*, a primitive insectivorous marsupial.

We may leave *Dasycercus* as an animal in the heyday of the power of the smell brain. And though we leave him in his burrow in the earth, we must not pity him; he is monarch of the world in which he lives. He has cunning superior to that of the lizards and the grasshoppers, he can overpower the young bird and in open attack can slay anything near his own size.

Nothing he can kill and eat is safe when he is near and hungry. More than that, he is capable of providing us with a brain which can teach us much of the story of our own.

CHAPTER XV

THE FALL OF THE SMELL BRAIN

The smell brain to which the mammals were heirs, and which is so triumphantly dominant in a well-equipped primitive mammal like *Dasycercus*, is not destined to hold sway for long. When we come to examine the story of the brain as it culminates in the production of the human qualities of cortical function we see a steady progress of the diminution of the sphere of the smell brain.

First councillor to gain place at the council table and first president of the fully represented council, scent is destined to be deposed in the dominant phylum of the mammals. Scent is dethroned when once the animal leaves the earth. The creature may take to the water, the air or the tree-tops, it does not matter which, so long as it leaves the earth to which the trail of scent clings. With us it was the tree-tops that provided the environment in which the animal became emancipated from the life-long bombardment of scents. Arboreal animals live in a sphere in which olfactory stimuli are relatively unimportant. Arboreal animals give up the fashion of possessing scent glands. They neither leave nor follow trails of scent.

But we must not forget that it is not only the loss of the importance of scent, it is the gain in the importance of other stimuli that is the great incentive for brain building. The animal must be prepared to learn as well as to forget. To be arboreal is not enough.

All animal stocks have not been in a position to grasp educational possibilities to the same degree; and a most instructive lesson may be learned from the examination of a series of brains of comparable animals representing respectively the marsupials and the higher mammals. If we compare the brain of the marsupial *Dasycercus cristicauda* with that of a non-marsupial Insectivore comparable to it in size and habit we meet with a most instructive parallel. *Hylomys suillia* is a shrew-like Insectivore which inhabits Mt. Kina Bulu in Borneo (see Figure 31). In size and in habit it is a match for *Dasycercus*. The brains of these two animals are singularly alike when viewed from the surface (see Figures 32 and 33). The brain of the marsupial is slightly larger than that of the higher mammal, but the amount of pallium devoted to smell and the amount devoted to other stimuli is very much the same in the two cases.

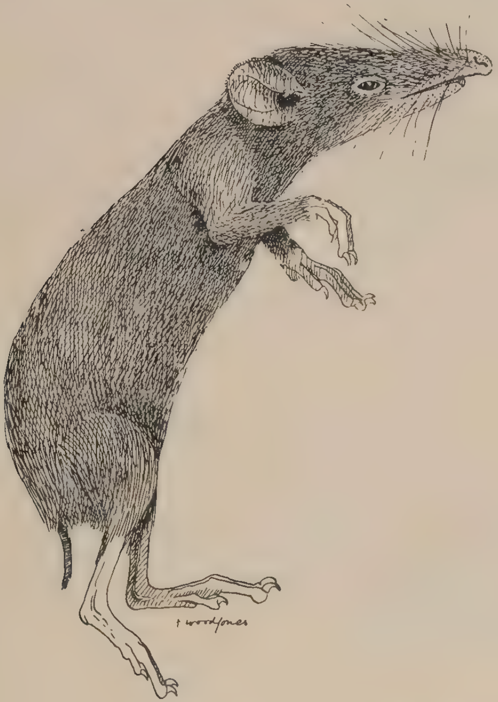


FIGURE 31.—*Hylomys*, a primitive insectivorous, non-marsupial mammal.

If we turn from this pair of comparable animals, representative of the two great mammalian phyla, to two slightly larger animals, which have become arboreal, we encounter a great change. The marsupial representative may fittingly be the ring-tailed opossum—*Pseudochirus laniginosus* and for a parallel among the higher mammals we may take a Bush-baby Lemur of about the same size—*Galago crassicauda.* Both animals are thoroughly arboreal, both are crepuscular or nocturnal in their activities. In general appearance they are somewhat alike, though the marsupial is rather the larger of the two. One glance at the two brains is enough to distinguish them. The smell brain of *Pseudochirus* is still large, occupying about one third of the whole pallial area (see Figure 34), whereas the smell brain of *Galago* is trivial in proportion when compared with the rest of the pallium (see Figure 35). Although *Pseudochirus* is a thoroughly arboreal animal it still has a very large proportion of its pallium devoted to smell, the pallium devoted to the other senses having lagged behind in a remarkable way when comparison is made with *Galago*. We may carry the parallels one stage further. The largest

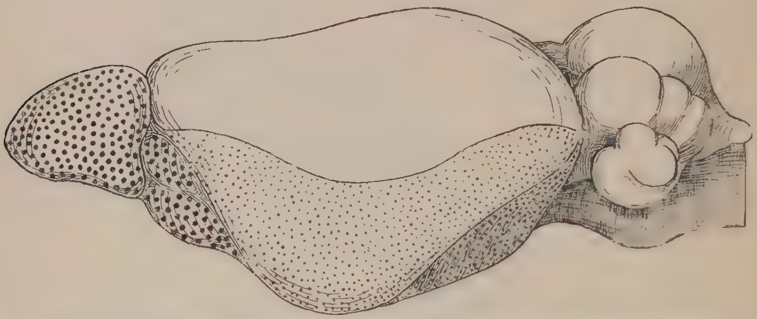


FIGURE 32.—The brain of *Dasycercus.* The portions of the brain connected with the olfactory sense are indicated by dots.

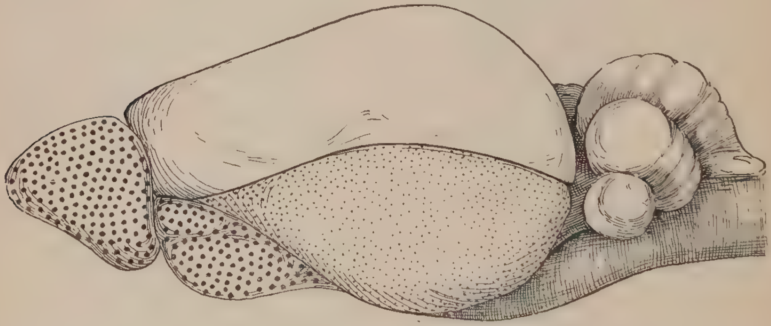


FIGURE 33.—The brain of *Hylomys.* The portions of the brain connected with the olfactory sense are indicated by dots.

and most perfectly adapted arboreal marsupial is the so-called Koala or Native Bear—*Phascolarctus cinereus*. In bulk we may compare it with a Patas Monkey, and even then the comparison is in favour of the Marsupial. Their brains are vastly different. The brain of *Phascolarctus* is not only ridiculously small (a point we will turn to later, but a large part of the whole pallium is still devoted to the sense of smell (see Figure 36). In the large pallial area of the brain of the monkey it is a hard task to find where the smell brain has disappeared (see Figure 37).

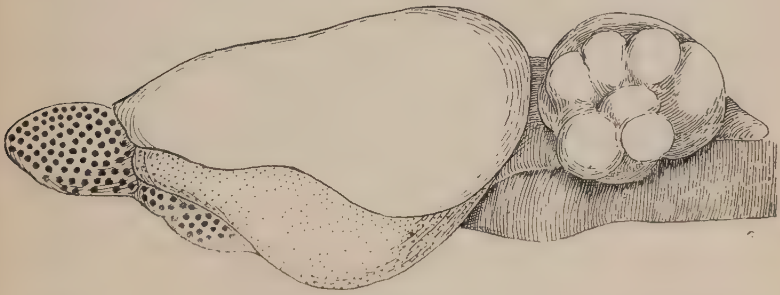


FIGURE 34.—The brain of *Pseudochirus*. The portions of the brain connected with the olfactory sense are indicated by dots.

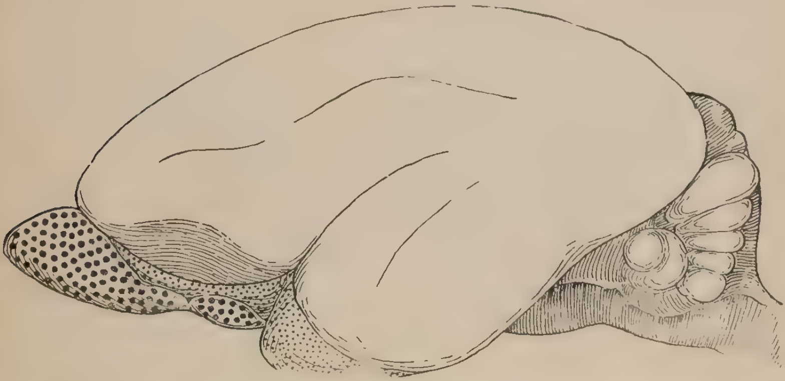


FIGURE 35.—The brain of *Galago*. The portions of the brain connected with the olfactory sense are indicated by dots.

These six brains provide a most interesting object lesson. We must admit the educational advantages of arboreal life, for we see them grasped by one phylum of the mammals. We cannot fail to see that arboreal life leads to a diminution of the dominion of scent. But granting all this, we have, in the marsupials, a great example of how a mammalian stock may fail to use its educational opportunities and remain slave to a guiding sense inherited as a birthright. It is, however, with the non-marsupial or monodelphian stock that we are concerned; for we ourselves belong to it. Here the study of brains of the Bornean Shrew—*Hylomys*, the African Bush-baby—*Galago*, and the Red Monkey—*Cerco-*

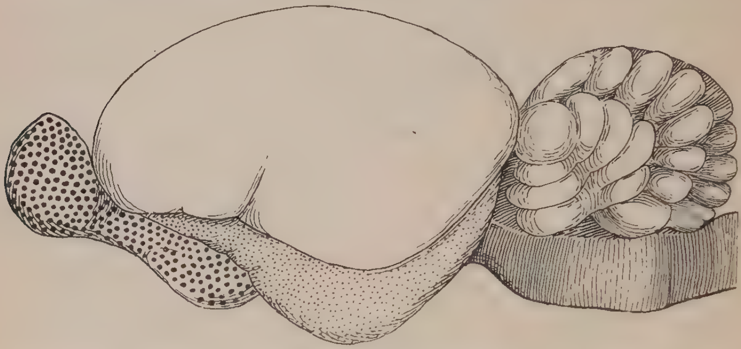


FIGURE 36.—The brain of *Phascolarctus*. The portions of the brain connected with the olfactory sense are indicated by dots.

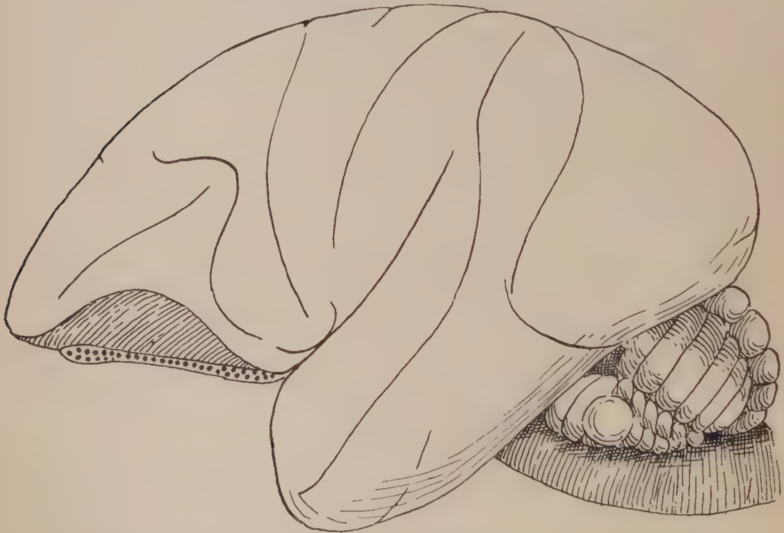


FIGURE 37.—The brain of *Cercopithecus*. The portions of the brain connected with the olfactory sense are indicated by dots.

pithecus, plainly tell their story. Their life in the branches has liberated them from the dominion of smell, they have had other avenues of learning opened to them and they have availed themselves of these opportunities and freed themselves from the tyranny of the olfactory sense. In *Hylomys*, *Galago*, and *Cercopithecus* we see a steady diminution in the extent of the olfactory pallium, until in *Cercopithecus* it becomes the merest rudiment, and in Man is a ridiculous apology.

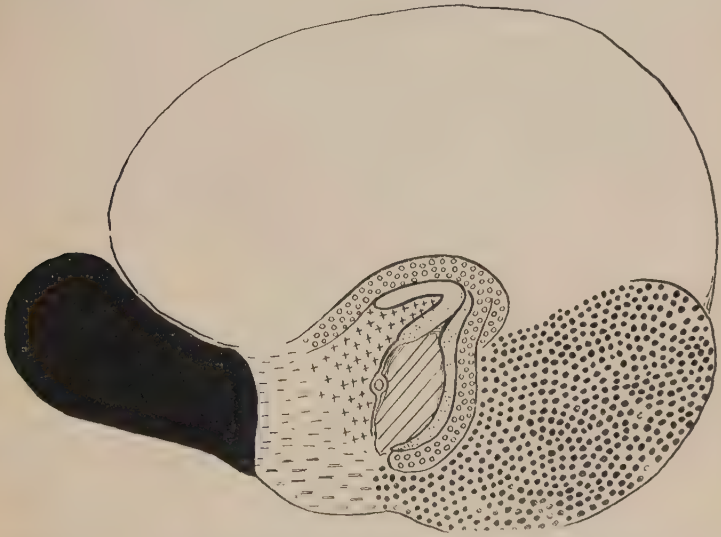


Figure 38.—Mesial surface of the right cerebral hemisphere of a typical mammal to show the parts of the brain constituting the Rhinencephalon. The non-olfactory parts of the brain are left white, the olfactory parts are distinguished by conventional signs employed in indicating similar parts in Figure 39.

The human olfactory pallium—the whole cortical area in which the impressions of smell are represented—what a despicable rudiment it is. In the basal members of the mammalian stock, we may safely say that a half and more of the pallium was given up to olfactory impressions, in us we should be generous if we say that one hundredth part of the whole area of the pallium was devoted to scent (see Figures 38 and 39).

The pallial rerepresentation area of smell has been driven from the map of the pallium as inferior races have been driven by advancing hordes of a more dominant people.

It has fled to the marches; it has been pressed to the farthest confines and, in our brains, holds minor sway along what may be termed the margins of the pallium.

Everyone, from personal experience, would be prepared to admit that the sense of smell was an undeveloped sense when compared with our other senses, and undeveloped when compared with the same sense in other animals. Probably few people would be prepared to find the parts of the brain connected with the olfactory sense so completely reduced and so thoroughly insignificant as they actually are.

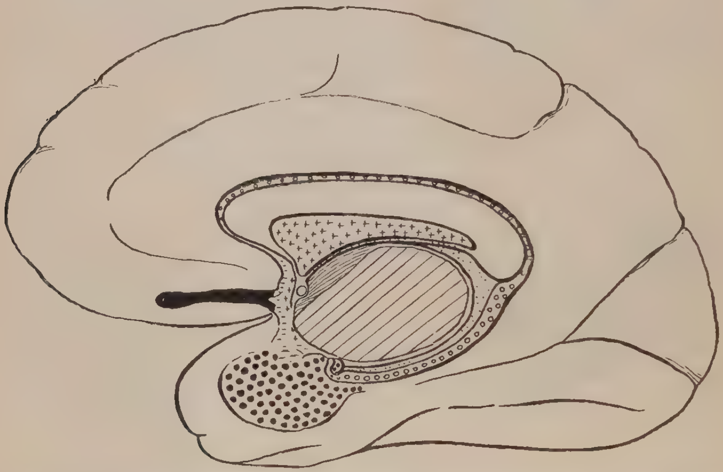


FIGURE 39.—Mesial surface of the right cerebral hemisphere of a human brain. The constituent parts of the rhinencephalon may be directly compared with those shown in Figure 38.

The whole of the parts of the brain which are devoted to the sense of smell constitute what is known as the *rhinencephalon*. For our purpose we may dismiss this rhinencephalon in the human brain by saying that it consists of a series of incoming nerves, ganglionic masses, connecting fibres and pallial areas, so much reduced that in any individual brain it is not always possible to find all the little rudimentary portions to which names have been given.

All parts of the rhinencephalon are driven from the lateral surface of the cortex and pressed to the opposed surfaces of the two pallial bubbles, where they become massed about the fibre masses that join the two hemispheres together.

Now, the sense of smell, like the sense of taste, but unlike our other senses, depends upon the chemical composition of the outside world. With touch, sight and hearing the case is different; it is the physical condition of the environment that appeals to our sense organs. The chemical composition of our environment is made known to us either by samples of it being carried in the air to our noses or by it being taken in bulk into our mouths.

The chemical sense is a lowly one and for the most part it informs the animal of what are intensely relevant though comparatively unaesthetic stimuli. It is the chemical sense that ministers to the two most primitive desires of the animal, for by means of this sense first the quest of food and then the dictates of the sex impulse are served. In the composite of chemical sense we include the olfactory impressions gleaned from the olfactory area of the nose, the stimuli gathered in some animals from the sensory epithelium of the organ of Jacobson, and the impulses derived from the numerous taste buds of the tongue and mouth. And indeed between the senses of taste and smell we are always in some degree of cortical confusion, for habitually we assume that we taste what in reality we smell. Taste and smell are twin senses and probably both as we know them are united in that sense which belongs to the organ of Jacobson.

In Chapter I we spoke of the origin of the central nervous system as being from those cells that had an experience of the environment: of set purpose we did not speak of epiblast. The student learns little when he assimilates the fact that this named layer of cells makes the brain as well as hair and horns and toe-nails. He is on the road to understanding more when he realizes that the qualification for becoming a cell of the central nervous system is the experience possessed by the cell of conditions of the environment. Since the chemical stimuli that we know as taste are derived from cells situated far within the body, it seems possible that some of these cells, though qualified by their opportunities for experience, might not be qualified by their epiblastic nature to become parts of the central nervous system. Here nature rises superior to the embryologist's diagrams: so long as a cell can learn of the environment it may be an informative cell of the central nervous system: nature does not share Haeckel's dogmatism for cell layers coloured blue and red and yellow in orderly diagrams. If a cell has anything to tell the central nervous system concerning the environment it is free to do so, even though it be a cell derived from hypoblast. If the mesoblast could be in touch with the outer environment doubtless it would also add its quota to the building of the central nervous system; but by its anatomical position it is denied that experience which alone is the real qualification. A hypoblastic placode is a thing easy to understand, since hypoblast may learn of outside things.

The stimuli of our chemical senses admit of no satisfactory classification, they admit of no analysis, nor do they inform us in any precise way as to the chemical composition of the substances which provoke the sensation. Our chemical stimuli tell us only vague and intangible things. There are no octaves or scales of scents or tastes: there is no dealing with these things in ordered fashion. Though the sense of smell is projected so that smells which are appreciated in our noses seem to be altogether without our bodies, yet we have no localizing mechanism. We may sniff: but we cannot tell right nostril impressions from left, in the way we may tell what is audible or visible to the ear or the eye of one side or the other. We may search about with our nose but we cannot attain to the distinctions of the wet-nosed mammal. The spatial relations of the stimuli are not appreciated by us.

Not only is the sense of smell sunk to a low ebb in us, but like all rudimentary things its development is very variable. In some persons it is much more keen than it is in others, and moreover there are certain odours which are appreciated by some which are never perceptible at all to a large section of mankind.

All this we must admit. Our sense of smell is degenerate, it is a vague, elusive and uncertain stimulus at the best of times.

The impressions we receive by our olfactory organs are not to be classified or localized: smell has ceased to be a guiding sense. We must also admit that the rhinencephalon is a ridiculous rudiment. Yet with all that granted, we must pause in wonder; for what a host of memories are crowded about the olfactory impressions which certain things convey to us. Probably there is no one who is able to smell at all, who does not have a whole series of associated memories clustered round and immediately evoked by some simple scent impression. Whole scenes may come imperatively to the mind upon the merest breath of some elusive odour. For some people scent is a master sense for memory and for association: and there is the marvel, that all these vast and complex memories have place in that narrow margin of the brain that constitutes our rhinencephalon. Truly a rudiment is our rhinencephalon, and a marvel of a rudiment for its physical function.

Yet though we may well be astounded at the myriad of smell memories that may be evoked from the pallium of smell, we may reasonably ask if these memories are precisely of the same rank as are those of, let us say, sight. I can remember a scent when I smell it again—even after a lapse of years. I can recognize the Pyramid of Cheops again after having once seen it years ago. I can shut my eyes and see the Pyramid of Cheops without being reminded of it by a fresh view of it. Can I remember the smell of violets, in the entire absence of any actual scent? Can I know a scent in its absence? Can I dream a scent? These are questions that would be answered differently by different people and the assertions on either side would remain unproven. Nevertheless it is not profitless to ask ourselves these things.

CHAPTER XVI

LINKAGES AND FAILURES

We have seen how, for some reason or other, the marsupial animals, though having educational opportunities similar to those offered to the animals which we regard as being upon our own line, have failed to take advantage of their arboreal station. Though many of them are as thoroughly arboreal as are any mammals, and though they have, therefore, had the opportunity of freeing themselves from the tyranny of scent and at the same time of gaining added information by touch, sight and hearing, they seem to have forgotten little and to have learned little during their sojourn in the branches.

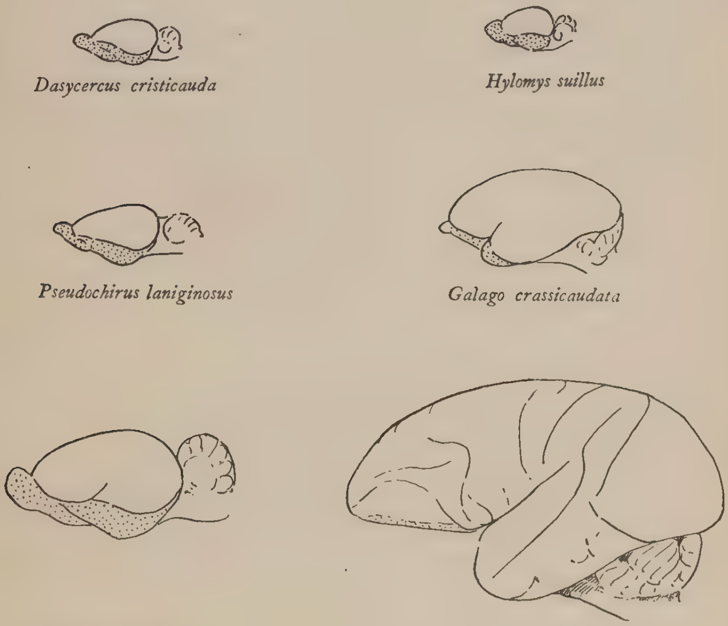
A young monkey will find its mother by sight or by hearing: but I have watched a young ring-tailed opossum track its mother up a bush, among its branches, and down again guided solely by the olfactory sense; for the mother had left that bush and gone to another some while before. Here is a clinging to an ancestral sense under circumstances in which other and more progressive animals have adopted newer and more instructive methods.

But it is not only in their clinging to olfactory impressions that the marsupials show themselves to be unprogressive; their greatest distinction is that the non-olfactory pallium remains so relatively undeveloped and as a consequence the whole brain is remarkably small.

Taking the same series of animals that we have already examined for the proportion of olfactory to non-olfactory pallium, we get a remarkable picture of the lag behind in development of the marsupial brain, if we take all the brains in their actual dimensions and contrast the marsupial and non-marsupial series (see Figure 40).

We have seen that the brain of the marsupial *Dasycercus* is slightly larger than that of the non-marsupial *Hylomys* though the animals themselves are practically the same size. In both cases the brain is in the region of 1/48 of the body weight.

If we take the next pair in the series we see at once that the brain of the marsupial *Pseudochirus* is far smaller than that of *Galago*, the actual ratio of brain weight to body weight in the two cases being about 1/150 and 1/50 respectively.



Dasycercus cristicauda *Hylomys suillus*

Pseudochirus laniginosus *Galago crassicaudata*

Phascolarctus cinereus *Cercopithecus patas*

FIGURE 40.—The relative sizes of the brains of a series of marsupials (left column), and higher mammals (right column). Each animal being comparable in body size to the example in the other series.

The last pair shows us the greatest contrast, for whereas the brain of *Phascolarctus* is only about 1/900 of its body weight, in the monkey it is about 1/125. A *Phascolarctus* has a ridiculously small brain which weighs only about 1/7 of that of a Patas monkey of the same size: moreover, as we have seen, this small brain is sadly lacking in non-olfactory pallium.

Pseudochirus is a thorough-going arboreal animal: it has had all the advantages and opportunities afforded by a life among the branches. Two sources of education it has perhaps not exploited, for it is nocturnal and light fearing, and it does not seek and pluck fruits but browses on tender shoots and young leaves. Despite its educational advantages it remains a remarkably unintelligent animal well enough adapted to living in the shelter of trees, with an abundance of food and an absence of enemies: but unsuited to change, competition, or adversity.

With *Phascolarctus*, specialization has proceeded further and the tree-climber has become a tree-clinger. Hands and feet have turned into hooks; and fingers are not used for plucking fruits or leaves or testing novel objects, but for fixing the animal, by virtue of the long curved claws, to the tree upon which it clings.

Since in our own phylum it is so easy to trace all the stages of advance in brain building, which seem so clearly to have their origin in the educational possibilities afforded by an arboreal life, it may well be asked: Wherein is the defect with the marsupials that their brains have lagged behind so strangely? There is surely something to be learned from the study of the brains of these two series; *Hylomys*, *Galago*, *Cercopithecus* on the one hand and *Dasycercus*, *Pseudochirus*, *Phascolarctus* on the other: something to give a clue as to the structural basis of the functional difference expressed in the fact that whereas the one series may culminate in the development of the brain of a man, the other produces the pitiable brain of the Koala.

It will be recalled that the whole nervous system begins to develop as a depression of the surface in the mid-dorsal line: part of it is derived from the surface of the right side and part from the left; there is a right half and a left half of the nervous system throughout its story.

When the pallial bubbles grow out from the brain stem they also are paired, there being a right-sided bubble and a left-sided bubble. At first these bubbles consist of nothing more than the olfactory cortex, but in the end they constitute the great cerebral hemispheres of man. These right-sided and left-sided pallial bubbles must obviously be kept in communication with each other, and for this purpose cell prolongations pass across the middle line, like the strands in electrician's wire, in the form of white fibre bundles. Bundles of this type, which connect different portions of the two sides of the brain, are known as *Commissures* (see Figure 41).

The first pallial developments, like the basal ganglionic masses from which they bud out, are connected by transverse fibres that run through the solid basal portion of the brain. These transverse fibres constitute a firm rounded cord embedded in the floor of the anterior end of the neural tube, and from its position this fibre bundle receives the name of *ventral commissure* (or, in human anatomy, anterior commissure). But as the bubbles of the pallium enlarge and grow upwards a new fibre tract unites their upper portions, and this fibre tract has the advantage of being free of the crowded structures of the floor of the brain stem. This commissure is known as the *dorsal commissure*. The dorsal commissure is free to expand, and especially to enlarge backwards with the growing cerebral hemispheres which it unites, and here it offers possibilities not afforded to the ventral commissure embedded, as it is, in the solid tissues of the brain stem.

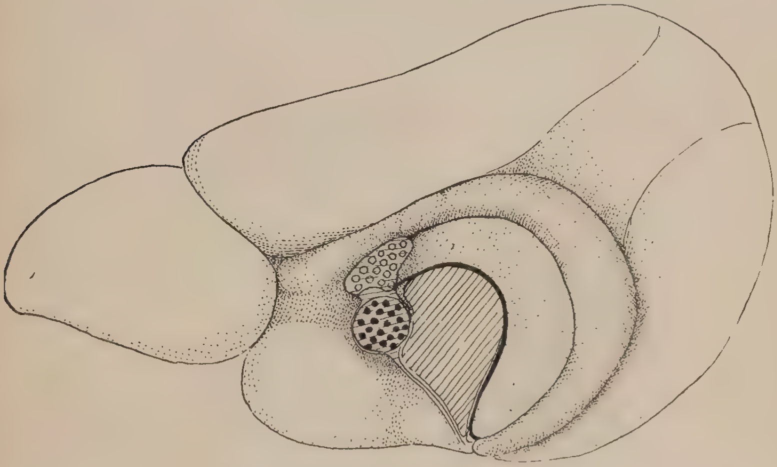


FIGURE 41.—Mesial surface of the brain of *Dasycercus* to show the commissures. In this figure and in figures 42, 43 and 44 the commissures are indicated by conventional markings. Black dots, ventral commissure; white circles, dorsal commissure; half-white circles, corpus callosum.

The dorsal portion of the pallium, therefore, finds in its new dorsal commissure a more direct linkage and one, moreover, capable of growth and readjustment. In the marsupials the dorsal commissure is usurping the place of the ventral commissure which is the dominant bond in the monotremes. But if the dorsal commissure of the marsupials must be regarded as large when comparison is made with the monotremes, it can only be considered as extremely small when comparison is made with the higher mammals.

In the marsupial *Dasycercus* (see Figure 41) the dorsal commissure is somewhat larger than the ventral commissure, and, unlike that bond, is not a simple round bundle of fibres like an electrician's cable. It is shaped something like a comma, with the concavity directed downwards and forwards. If we turn to the brain of the monodelphian *Hylomys* we find that this bending of the dorsal commissure has become much more marked, and that now the fibre bundle has become shaped like a horseshoe magnet with the two limbs pointing forwards (see Figure 42). In *Hylomys* there is a dorsal limb and a ventral limb in the dorsal commissure—there is a differentiation in structure.

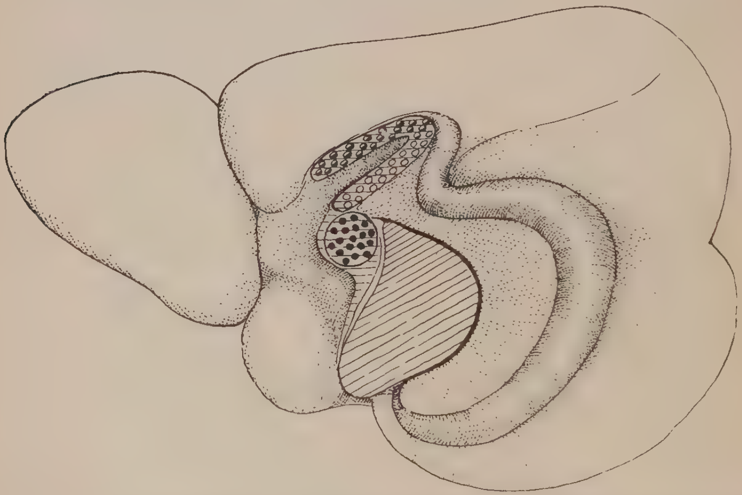


FIGURE 42.—Mesial surface of the brain of *Hylomys* to show the commissures. The corpus callosum has developed as a dorsal limb of the dorsal commissure.

Returning to the marsupials and appealing to the brain of *Phascolarctus* we see the dorsal commissure much in the form that was noted in the case of *Dasycercus*. The hooked arrangement of the commissure is somewhat better marked, but there is no specialization into dorsal and ventral limbs such as is present in *Hylomys* (see Figure 43). The monodelphian parallel to *Phascolarctus* we have selected in *Cercopithecus* and when we turn to the brain of our Primate type we notice a profound change.

In the first place, the mass of the dorsal commissure is vastly greater than that of the ventral commissure and in

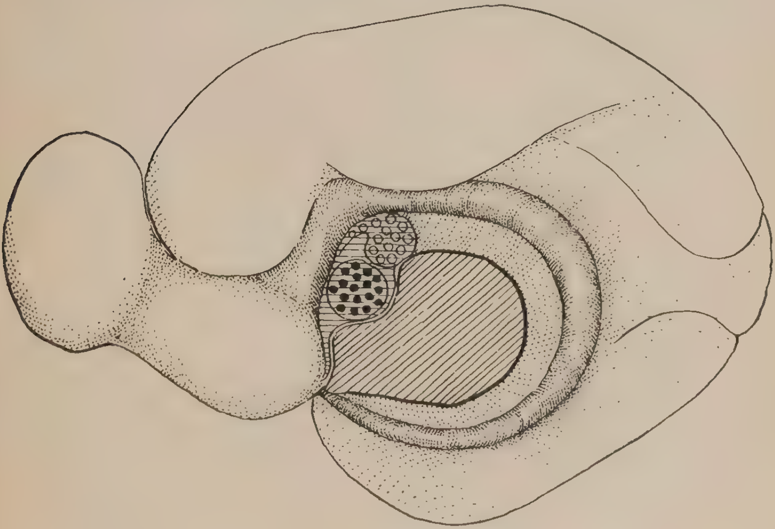


FIGURE 43.—Mesial surface of the brain of *Phascolarctus* to show the commissures.

the second place the dorsal commissure has become extremely specialized by the development of its dorsal limb. We may learn then from a study of our marsupial and non-marsupial parallels that not only does the general brain growth of the marsupials lag behind, but that the dorsal commissure in them fails to undergo the growth and specialization which is typical of the higher mammals. These things are evidently correlated.

We have noted that in passing from *Dasycercus* to *Pseudochirus* and to *Phascolarctus* there is a failure of progress in brain development with increase of body size and perfection of arboreal adaptation. We have noted how in passing from *Hylomys* to *Galago* and to *Cercopithecus* the whole brain, and especially the non-olfactory pallium, has developed by leaps and bounds.

The lag behind on the one hand, and the rise to supremacy on the other, are evidenced not only in the gross development of the pallial areas but in the fibre bonds which unite them across the middle line. The marsupial fails in its pallial bonds. The dorsal commissure remains comparatively simple though it may considerably exceed the ventral commissure. In the marsupials with the best-developed brains the dorsal commissure is no more than a simple comma-shaped fibre bundle. In the higher mammals the dorsal commissure becomes differentiated into two structures which in human anatomy are known as the *Corpus callosum* and the *Fornix* (see Figure 44). The corpus callosum is the name for the large dorsal part of the horseshoe-shaped fibre bundle, the fornix is the name for the diminishing ventral limb (see Figure 20). It is the corpus callosum that is rising to supremacy along the line of animals assumed

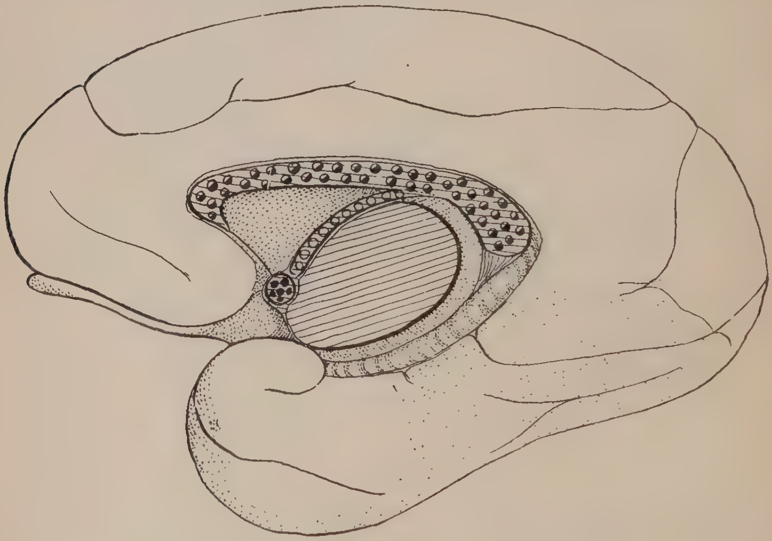


FIGURE 44.—Mesial surface of the right cerebral hemisphere of *Cercopithecus* to show the commissures.

to be upon our own ancestral tree: it is the corpus callosum that fails to develop in the marsupials.

It is the corpus callosum that in the higher mammals becomes specialized as the commissure that links the non-olfactory pallial areas of the right and left sides; the olfactory areas remaining linked by the fibres of the fornix.

We may say, therefore, that for perfection in brain building, in so far as it has been carried in the mammals, we need, in addition to the ancestral ventral commissure, a dorsal commissure which shall develop a specialized dorsal limb in which are the fibres linking the non-olfactory portions of the pallium. This dorsal, non-olfactory limb is known as the corpus callosum and as such it fails to develop in the marsupials.

The question of the corpus callosum is historic. Battles were waged concerning it: battles instructive of the times in which they were waged, and in which might has not always been with the right. The days of the fight are done with and we may say that the development of a true corpus callosum takes place only in the higher, non-marsupial mammals. The marsupials have as their hall-mark this failure, that the corpus callosum—the great, dominant fibre tract connecting the all-important non-olfactory parts of the pallium—did not develop in their phylum. Here then is another story of failure in brain building. The lowest mammals, represented by the monotremes, possessed a large ventral commissure and a relatively small dorsal commissure. The marsupials developed the dorsal commissure to a greater degree, but failed altogether to effect the structural modification which begets a true corpus callosum. They are failures. Wherever marsupial meets higher mammal it is the marsupial that is circumvented by superior cunning and forced to retreat or to succumb. Marsupials fail because their cerebral development is arrested, they cannot cope by intelligence, by cunning or by artifice with the superior gifts of the higher mammals. The fox, the cat, the dog, the rabbit, the rat and the mouse are all ousting their parallels in the marsupial phylum; ousting them because they have developed that specialized dorsal non-olfactory bond of the pallium which we term the corpus callosum. Here then is another lesson. We have learned of the failure of the brain development in Invertebrates; we have seen that, even in the lower Vertebrates, mistakes seem to have been made in the architecture of the central nervous system. When we arrive at the mammals all is not simple or assured, for the monotremes with all their cortical development have lagged behind in linkages; the marsupials have failed, and their failure seems to be wrapped up in their lack of a corpus callosum. Here again the brains of the marsupial *Dasycercus* and the non-marsupial *Hylomys* are of the utmost importance. How little it takes to convert the bonds of the one into those of the other: how great are the possibilities of the conversion. Separate the dorsal portion of the dorsal commissure: give the non-olfactory portions of the pallium their own pathway: make a corpus callosum, and the higher brain is achieved.

But the marsupials never perfected these apparently simple evolutions and, for lack of development of a corpus callosum, remained a failure.

Since the corpus callosum is obviously of such great importance in the phylogenetic series of the mammals, it might be expected that there would be abundant experimental evidence as to the exact rôle that it played in bringing about the advance of those mammals in which its development was initiated. We know that it is a huge commissural tract and that it unites the more important areas of the pallium of the two halves of the brain; so much is evident from the anatomical study of the disposal of its constituent fibres. We know that the animals lacking the tract are not so well endowed as are those possessing it; but this does not furnish us with any very real understanding of its functions. Moreover human beings at times fail to develop the typical disposition of their fibre tracts and so lack a true corpus callosum, nor has any functional indication of this anatomical anomaly been detected during the life of those individuals whose acollosal brains have been discovered at post-mortem examination. It is by the method of conditioned reflexes that most light has been thrown upon the functions of the corpus callosum. If a normal dog has been trained so that it is accustomed to associate the receipt of food with a certain stimulus applied to a definite point upon one side of its body, it will secrete saliva in anticipation of the food every time that particular spot is stimulated. When the other spots upon the same side of its body are stimulated no secretion follows. There is only one other spot the stimulation of which will produce the reaction and that is the exactly corresponding point upon the opposite side of the body. If now the dog's corpus callosum be divided it will still respond to stimulation of the original spot, but stimulation of the corresponding point on the opposite side fails to produce the response.

This may not seem to be a very important rôle for this great fibre tract, but evidently the function which is demonstrated by this experiment is that of correlating and co-ordinating the two sides of the body within the pallium. Deprived of the corpus callosum, the dog has suffered some disintegration of the perceptions, since it has ceased to be able to correlate corresponding portions of the two sides of the body. |Now the function of correlating the two sides of the body is no mean thing, for it is a vast step in that dominant enterprise of the central nervous system—the integration of the pallial perceptions of the various parts of the body into one complex whole. As we shall see later, complete integration of the whole individuality in cortical terms is the triumph of the human brain. This triumph was made possible by the development of the corpus callosum from the dorsal commissure in the lowly monodelphian mammals.

CHAPTER XVII

SENSATION AND THE LOWEST SENSORY NEURON

The power to feel—the manifestation of the function of sensation—is a phenomenon inherent in all living matter. The ability to respond to stimuli is a property of protoplasm itself and every living cell in the whole complex organization of an animal body is potentially capable of sharing in this common attribute.

But in speaking of sensation as a function of a complex living animal we are dealing with the impulses that are generated by stimuli in sensory cells and from these sensory cells are carried by the peripheral sensory nerves to the central nervous system, rather than with the simple ability of protoplasm to react to a stimulus. Sensory cells, as we have seen, are, for the most part, those that have as a birthright a special sensitization to the things of the outside world—those of the outer surface of the animal, or, as we have termed them, the cells of the external nervous system. It is the skin of the outside of our bodies that tells us, by the medium of common sensation, our relation to external things. Such a quality of sensation is termed *superficial sensibility*. But in addition to this, we have also an appreciation of certain deeper parts of the body, such as our joints and muscles, and this is termed *deep sensibility*.

Now all sensibility is not of the same kind, and though the two elements which enter into its composition are not very easy to define they are extremely easy to appreciate in the recovery of nerve injuries as that process is manifest in man. There is as one component of superficial sensibility, an underlying crude, primitive sensibility to contact; an undiscriminating, unlocalized knowledge that the sensory surface of the body is being interfered with. In the case of deep sensibility this component is expressed in the appreciation of pressure pain or the recognition of the unpleasant element of pressure. Despite the doubts that have been cast upon it by some physiologists, the reality of this element is far more thoroughly verified to-day than it was when Head first described it nearly twenty years ago. To this element of sensation Head gave the name *Protopathic Sensibility*. Protopathic sensibility, which is so well demonstrated in cases of recovering nerve injury in man, consists in a crude, uncritical appreciation of stimuli, which are, as a rule, painful, unpleasant or undefined and are always crudely affective. Even when protopathic sensibility is manifested in impressions that are not unpleasant, the pleasurable sensation is crude and indescribable. Protopathic sensibility is not precisely localized. The exact spot where the stimulus is inflicted is not realized, and moreover the sensation tends to radiate from the site of infliction and to be appreciated over a wider area than the spot actually stimulated. Neither is protopathic sensibility graded; the appreciation of the stimulus bears little relation to the intensity of the stimulus, for any adequate stimulus will produce a high degree of appreciation.

There is every reason to believe that this is a primitive form of sensation—the feeling that the animal is being interfered with by outside stimuli, the exact site of the stimulus and the exact nature of the stimulus being not very rigidly defined. The animal is aware of an interference with its sensory surface or is aware that its movements are being restrained or that its parts are being subjected to pressure and this interference is usually of a harmful nature.

In every way, protopathic sensibility is crude, unaesthetic and utilitarian. It is the sensory impression that produces defence reactions, as when an animal withdraws a limb to which a noxious stimulus is applied. It indicates to the animal a change in the affective stimuli reaching the part. Just as it is primitive and old established so it is the first element of sensation to reassert its activity after a nerve has been injured and a part of the skin and the deeper tissues thereby rendered insensitive.

In man this old form of sensibility has been so completely dominated by the newer element of sensation that it is difficult to realize its exact quality. Nevertheless there is in man a territory that is exclusively protopathic in its sensation. The terminal portion of the male genital organ is endowed only with protopathic sensibility, there being none save the old, crude, undefined sensations capable of appreciation by that part of the human body. It is among the lower vertebrates (and in incompletely recovered nerve injuries in man) that protopathic sensibility is seen so dominantly.

In the higher vertebrates another element of sensation is manifested and this, following Head's terminology, is termed *Epicritic Sensibility.*

As opposed to protopathic sensibility, epicritic sensibility is an aesthetic, discriminative, localized and graded sensibility; it is the sensation with lights and shades, the sensation with degrees of appreciation, and which demands a considered and graded response. Epicritic sensibility is something added to protopathic sensibility, but by its very discriminative nature it may be said to overlie and mask the cruder nature of the older form of sensation. Epicritic sensory impressions do not find their motor outlet in stereotyped defence reflexes, but rather in considered purposive actions which are graded and adjusted to the precise nature and precise localization of the stimulus.

When a human nerve, which has been injured, recovers its functions, it is the protopathic sensibility that first returns, the epicritic sensibility being restored later and often less completely. Epicritic sensibility, for the purposes of practical investigation, is tested for by means of the very lightest touch of cotton wool upon the surface of the skin, or by the ability to appreciate cold and heat between the limits of 26° and 37°C. Protopathic sensibility is manifested by the appreciation of the prick of a sharp needle or the perception of degrees of cold and heat beyond 26° and 37°C. In the case of deep sensibility the epicritic element is represented in the appreciation of the position of joints and parts and in estimating the degree of passive movement. It is shown in the recognition of the increments of pressure and in the direction, localization and range of movement of a part. Sensibility, therefore, is complicated in that it has a dual nature in the coexistence of the primitive protopathic element and the overlying epicritic factor; it is also complicated by the fact that it is compounded of superficial sensibility, derived from the skin surface and from the hairs which clothe it, and deep sensibility, derived from joints, muscles and deeper structures.

We may, therefore, divide common sensation into protopathic and epicritic constituents and distinguish the two groups of superficial and deep sensibility, but it is also necessary to class sensations in those categories of the named qualities in which they are appreciated. We can distinguish touch, pain, heat and cold, pressure, sense of position and sense of vibration as well-defined entities of common sensation.

Again, these qualities may be compounded in what has been termed the stereognostic sense, which enables us to appreciate the size, shape, and nature of objects touched or handled.

Such a classification is functional or physiological, but it is almost certainly an anatomical grouping as well, since the different qualities of sensation are probably derived from the different terminal organs of the sensory nerves. There are many ways in which sensory nerves end in the skin, subcutaneous tissues, joints, and muscles. These sensory end-organs vary from the minute terminal twigs of sensory nerves, which constitute an infinitely fine meshwork among the cells of the skin, to such elaborate structures as Meissner's corpuscles, Pacinian bodies and many other named types. The complexity of the qualities of sensation would seem readily matched by the multiplicity of the types of sensory end-organs or receptors.

When sensation is evoked, a stimulus is imparted to the sensory end-organs and from here starts upon its journey towards the brain and towards recognition. The nerve fibre that carries the stimulus upwards is a long, continuous, protoplasmic extension of one of those cells which, lying towards the edge of the embryonic neural groove, was one of the last recruits to the nervous system and, therefore, sensory in function. This long protoplasmic filament of the cell is one of the many such filaments, each derived from its parent cell, which are gathered together into a bundle constituting an anatomical nerve. In this nerve all the filaments are not derived from sensory nerve cells, for some are extensions of cells which, originally situated nearer to the middle line of the neural groove, are motor in function. Some filaments in the mixed nerve are carrying impulses centrally to the central nervous system and these are the *afferent or sensory fibres*; some are carrying impulses from the central nervous system towards outlying parts and these are *efferent or motor fibres*. The best name for these protoplasmic extensions of nerve cells, which constitute the individual filaments of anatomical nerves, is *neuraxon* and this term will be adhered to throughout. Now we have seen that in the inception of the nervous system the sensory nerve cells were towards the margins of the neural groove and the motor nerve cells were situated towards the middle line. We have also seen that when the groove becomes infolded to form a tube—the spinal cord—the sensory nerve cells are on the dorsal and the motor nerve cells on the ventral aspect of the spinal cord. In order to reach their parent nerve cells, the neuraxons in a mixed nerve have, therefore, to sort themselves out as they approach the spinal cord. They sort themselves out into what are called the posterior or dorsal root and the anterior or ventral root of the nerve. By the anterior root the motor neuraxons pass to their parent cells within the anterior portion of the spinal cord. By the posterior root the sensory neuraxons pass to their parent cells which are situated, not within the tissues of the spinal cord itself, but in the ganglion situated upon the posterior root.

The cell in the posterior root ganglion—the sensory cell turned in with the infolding of the neural groove—has two main protoplasmic processes; one is the neuraxon that passes towards the surface of the body in a bundle of neuraxons constituting a nerve and the other is one that runs in the opposite direction, by way of the posterior root, into the tissues of the spinal cord itself.

A sensory impulse can, therefore, travel from the sensory end-organ in the skin to the posterior root ganglion cell and thence, by another extension of the cell, to the spinal cord.

This posterior root ganglion cell and its two neuraxons, the one running peripherally and the other centrally, constitute a living entity—a cell with two elongated pseudopodia.

It is the cell, which was tucked in from the surface of the body, stretching out a long process in one direction to keep it in touch with the knowing cells of the surface of the body and another process in the opposite direction to keep it in touch with the other constituents of the internal nervous system. This entity is known as the *lowest sensory neuron.*

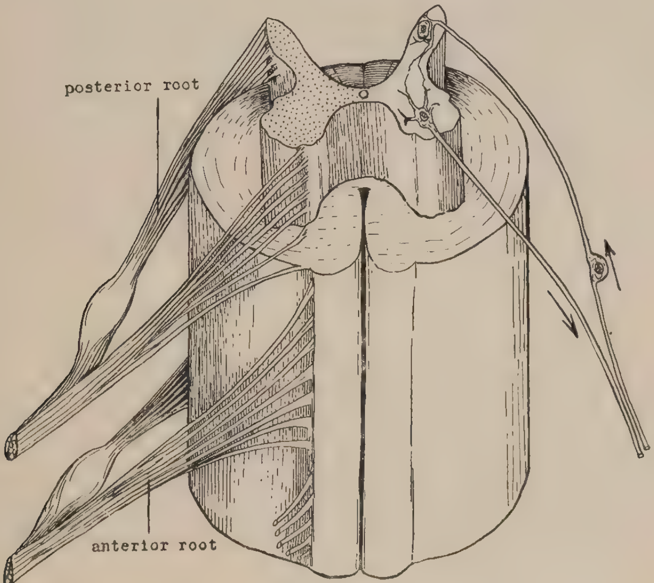


FIGURE 45.—Diagram of a portion of the spinal cord to show the anterior and posterior roots of the spinal nerves. In the upper part of the diagram the grey matter of the cord is represented as sculptured out from the white matter.

The centrally running neuraxon of the lowest sensory neuron runs to the spinal cord by way of the posterior root of the spinal nerve and it enters the cord on its posterior aspect, joining what is called the posterior column of the cord. Having embedded itself in the tissues of the cord it gives off fine processes, or dendrons, which run forwards to the front of the cord and make connection with the motor nerve cells of the anterior horns of the spinal cord grey matter (see Figure 45). These are the primary links between the original sensory nerve cell and the original motor nerve cell. By these linkages the incoming sensory impulse may affect a group of motor nerve cells in its neighbourhood and so pass on an impulse through their neuraxons to the end plates in the muscles—and thus become translated into movement: they form the anatomical pathway of a *spinal or lowest level reflex.*

Reflexes that are carried out by means of the interconnection of sensory neuraxons and grouped motor cells in the spinal cord may be extremely elaborate in lower vertebrates, but in us they have largely lost their importance. It may be almost as difficult to capture a decapitated chicken as to secure one controlled by its brain and guided by its sense organs. A snake from which the head and much of the anterior end of the body have been blown clean off by a gun may yet perform the most complicated movements. Obviously in these creatures there is a great deal of coordination carried on at the lowest level by the grouping of motor and sensory cells and axons in the spinal cord. In the higher vertebrates, and especially in man, the lowest level reflexes are of lesser importance; nevertheless they may be readily evoked and we need only instance the bending of the joints of the leg, bringing about a withdrawal of the foot when the sole is tickled.

The dendrons which the central neuraxon of the lowest sensory neuron gives off to the motor cells of the spinal cord are only offshoots from the main neuraxon, which itself continues on its way upwards in the posterior column of the spinal cord and ends by coming into communication with a nerve cell in the posterior horn of the grey matter of the spinal cord.

This is the end of the lowest sensory neuron. The lowest sensory neuron, therefore, extends from a sensory end-organ in the skin or subcutaneous tissues to its parent cell in the posterior root ganglion and thence by another neuraxon to the spinal cord where, after having given off dendrons to the motor cells in its neighbourhood, it ends by arborizing around a cell in the posterior horn of the same side.

From an end-organ in the skin of my right little finger a neuraxon runs upwards with a leash of others that constitute the ulnar nerve in my right arm. From the ulnar nerve this neuraxon passes into the brachial plexus and thence to the posterior root of the eighth cervical nerve. It joins its parent nerve cell in the posterior root ganglion and from this cell another neuraxon runs in the posterior root to the spinal cord where it ends, after giving dendrons to motor cells, by coming into communication with a nerve cell in the posterior horn of the right side of the spinal cord.

Such is the ground plan of the disposition of all lowest sensory neurons; but concerning the actual details of their course within the spinal cord there is some variety displayed and in this variety lies the interest and the beauty of the arrangement.

CHAPTER XVIII

THE SECOND SENSORY NEURON

The centrally running neuraxon of the lowest sensory neuron runs to the posterior column of the spinal cord and so finds its end in a synapse about a posterior horn cell of that side of the cord on which it entered.

All lowest sensory neuraxons are alike in this method of termination; nevertheless, there is much variation in the precise details of their course. This variation affects the length of their upward journey in the posterior column of the spinal cord. Some lowest sensory neuraxons come to an end by effecting a synapse with a posterior horn cell almost immediately upon entering the posterior column; some run a short distance upwards in the posterior column before they end around a posterior horn cell and some run the whole length of the posterior column before they make a synapse about the cell of the second neuron and so find their goal. At whatever level the synapse is, there is the end of the lowest sensory neuron.

The cell round which the synapse takes place is the start of the *Second sensory neuron*. From the parent cell of the second sensory neuron, the neuraxon passes across the middle line of the spinal cord in the grey commissure and so comes to take up its station in the lateral column of the opposite side of the cord; and in this column it continues its course upwards (see Figure 46).

Although the unravelling of the course of any particular neuraxon may appear to be an extremely complicated affair, there is, nevertheless, a general principle that underlies all the complexities of the sensory tracts within the spinal cord.

The end attained by these apparent intricacies is a regrouping of the neuraxons, and a reclassification of the stimuli they are conveying to the higher centres of the central nervous system. *The quality of sensation carried by the lowest sensory neuron is not the quality of sensation carried by the second sensory neuron.* The peripheral nerves of the lowest sensory neuron carry a dual superficial system of epicritic and protopathic sensibilities, as well as the dual components of deep sensibility and the various elements of spatial realization. The lowest sensory neuron can inform the higher centres of the sensation of pain, but pain may be the product of either the protopathic or epicritic or of the superficial or deep constituents of the lowest sensory neuron. The lowest sensory neuron is a road of mixed

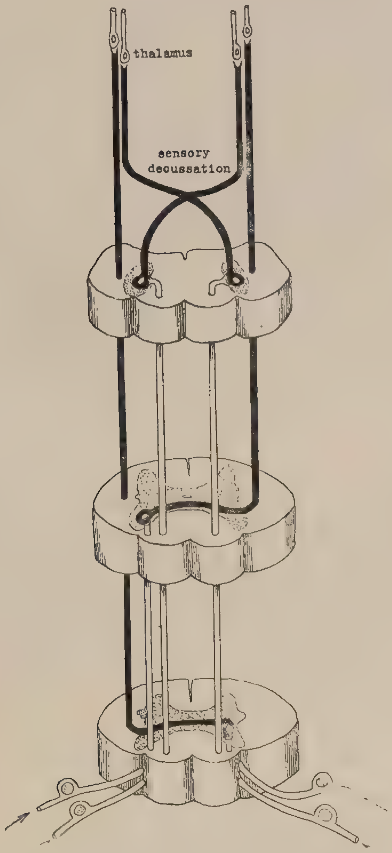


FIGURE 46.—The sensory pathways in the spinal cord. The lowest sensory neuron is white: the second sensory neuron, black.

traffic by which several components of a quality of sensation are carried to the posterior horn cell. The second sensory neurons are pathways of specialized stimuli by which the sorted components of sensation are carried to the higher centres. The business, therefore, of the readjustments in the spinal cord is that of sorting out sensations from the welter of the myriad instreaming impressions carried by the lowest sensory neurons. The purpose is to sort out all sensations of one kind from the mixed sensations carried by the lowest sensory neuron.

Now lowest sensory neuraxons travel in the posterior column of their own side of the spinal cord for a longer or shorter distance before they come to an end by forming a synapse about a posterior horn cell of that side of the cord. They travel in the posterior columns of their own side as unsorted lowest neuron fibres carrying unsorted lowest neuron stimuli. Directly they meet their destined posterior horn cell of their own side of the cord and end in a synapse their individuality is lost. From the posterior horn cell the second sensory neuraxon crosses to the lateral column of the opposite side of the cord and runs upwards as a sorted second sensory neuraxon carrying sorted second neuron stimuli.

It, therefore, follows that, at any given level of the spinal cord, the posterior columns of one side of the cord will contain unsorted lowest neuron fibres and the lateral column of the opposite side will contain sorted second neuron fibres from the same region of the body. Herein lies the clue to the understanding of all sensory effects of lesions of the spinal cord. This sorting of the stimuli carried by the lowest sensory neuron takes place at different levels in the case of different stimuli. Some of the lowest sensory neuraxons come to an end in their synapse almost immediately upon entering the posterior columns of the spinal cord. They come in by the posterior root, enter the posterior column, and almost immediately synapse around a posterior horn cell and so end. Some enter by a posterior root, run a short distance upwards, synapse around their destined posterior horn cell and so cease as lowest sensory neuron fibres. In general, it may be said that those lowest sensory neuraxons that carry stimuli of pain run the shortest distance in the posterior column of their own side before ending in a synapse with a posterior horn cell. Those carrying temperature stimuli run an almost equally short course, before they pass to the opposite side of the cord as second sensory neuraxons. It is thus true to say that the sensations of pain and of temperature are sorted, classified and grouped in the second sensory neuraxons running upwards in the lateral column of the opposite side of the cord very soon after the entry of the lowest sensory neuraxons into the posterior columns of their own side.

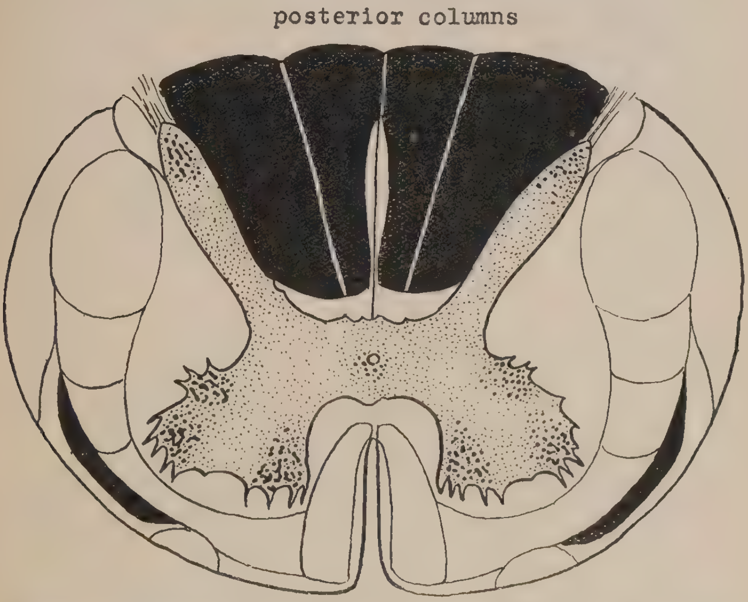


FIGURE 47.—Diagrammatic section through the spinal cord to show the various spinal tracts. The sensory pathways are black.

Sensations of touch and the appreciations of contact run further as unsorted lowest sensory neuraxons in the posterior column of their own side of the cord. The method of sorting is, therefore, that different fibres run shorter or longer courses as unsorted lowest sensory neuraxons in the posterior column of their own side, with consequent longer or shorter courses as sorted second sensory neuraxons in the lateral column of the opposite side of the cord (see Figure 47). The sorted second neuron fibres travelling upwards in the cord constitute a tract in the lateral column known as the *spino-thalamic* tract; since by this tract the fibres of the second sensory neuron are carried from the lateral column of the spinal cord to the great nerve cell mass in the brain stem known as the *thalamus*. After the spino-thalamic tract has reached the upper limit of the spinal cord it traverses the brain stem, still as a discrete bundle of fibres, in the tract known as the *medial fillet* (lemniscus medialis). By the medial fillet the second sensory neuron fibres are carried to the thalamus, around the nerve cells of which the second sensory neuraxons synapse. In this synapse the second sensory neuron comes to an end.

Such is the fate of the spino-thalamic tract of sorted second sensory neuron fibres from the lateral columns of the cord to the thalamus; but we have already noted that some lowest sensory neuraxons travel intact, unsorted, and uncrossed in the posterior column to the upper limits of the spinal cord. The fibres that make the long pilgrimage of the posterior columns as lowest sensory neuraxons are those subserving certain elements of touch. These elements will be more precisely defined, but in the meanwhile we are in a position to postulate the effects that would be produced by lesions of the upper end of the spinal cord. If the upper extremity of the spinal cord is cut half through on the right side, painful and thermal stimuli will not be appreciated on the left side of the body, for the spino-thalamic tract of the right side is severed, but impressions of touch may be but little disturbed on the left side. On the right side of the body, however, there will be a gross loss of the discriminative elements of touch, for the right posterior column has been severed: but thermal and painful stimuli will be appreciated.

Those fibres concerned with touch, which make the longest journey as lowest neuraxons in the posterior column, are those that may be described as discriminative. These discriminative touch fibres and those subserving the appreciations of joint sensibility, of spatial relations and of pressure run as the longest neuraxons of the lowest sensory neurons in the posterior columns. They continue on their own side until the spinal cord comes to an end, and they do not form synapses around posterior horn cells, but around the cells of the ganglionic swellings situated at the summit of the spinal cord and known as the *nucleus cuneatus* and *nucleus gracilis*. These fibres are, therefore, still left upon the side of the cord on which they originate when the cord has come to an end. The neuraxons of the second sensory neurons which originate in the nerve cells of the nucleus cuneatus and nucleus gracilis have, therefore, to cross to the opposite side in the brain stem instead of effecting their crossing in the spinal cord. They run upwards in a bundle as the *internal arcuate fibre tract* and their crossing is made after they have joined the fillet by what is known as *the decussation of the fillet or sensory decussation*. Having crossed in the decussation of the fillet these fibres behave as the other fibres in the non-decussating portion of the fillet and end by joining a synapse around a nerve cell in the thalamus.

All second sensory neuraxons, therefore, cross to the opposite side of the body on their journey upwards to the thalamus. Some cross early in the grey commissure of the spinal cord, some cross at higher levels by the same route and all of these continue to the thalamus in the direct, non-decussating portion of the fillet. Some, however, subserving mainly discriminative and spatial impressions are begot so high in the cord that the grey commissure is not available to them as a route for crossing, and these fibres pass from their own to the opposite side of the body in the decussation of the fillet in the mid brain.

All the different fibres with which we have so far dealt produce, in the central nervous system, impressions of sensation, the impulses enter into consciousness and we are aware of them; but all the upstreaming fibres conveying impulses from the second sensory neurons do not carry stimuli which force their way into our recognition as sensation. There is in the posterior column of the cord a large constituent of what may be termed *silent afferent fibres* and these do not make passage of the fillet and end in the thalamus. The silent afferent fibres of the posterior columns run to the cerebellum and not to the fillet and the thalamus, and do not force their way to the level of consciousness. These fibres convey afferent impulses from muscles and joints and deep tissues: they constitute the afferent side of the co-ordinating mechanism for the control and regulation of poise and balance. We are not aware of their stimuli but, nevertheless, they are constantly surging upwards to the cerebellum, constantly creating those impulses by which the body is kept balanced and poised and by which the movements of muscles and joints are co-ordinated without the intervention of consciousness.

The story, then, of the second sensory neuron is that it replaces the lowest sensory neuron and passes away to the opposite side of the body. The passing away occurs at different levels and in general terms we may say that the more crudely affective is the quality of the sensation, the earlier is the yielding of the lowest sensory neuron to the second neuron and the lower the level of the crossing: whilst the more discriminative and the less affective the quality of the sensation, the later is the yielding of the lowest sensory neuron, and the higher the level of the crossing.

CHAPTER XIX

THE HIGHEST SENSORY NEURON

Judging from the wealth of sensory neuraxons that stream upwards in the fillet and find their goal in the cells of the thalamus, we should be justified in supposing that this great ganglionic mass in the brain stem should be regarded as an important sensory receptor. Of the function of the thalamus as a sensory cell station there is no doubt. It is the cell station in which the second sensory neurons of the opposite side of the body terminate by synapse around a thalamic nerve cell. Sensory stimuli are carried to the cells of the thalamus by the second sensory neurons. This is not, however, the final cell-station of all the elements of the sensory tract, for from thalamic cells new neuraxons pass towards the so-called sensory pallium of the post-rolandic or post-central region of the cortex. These neuraxons are known as the *thalamo-cortical* fibres and the thalamic cell and its pallial neuraxon constitute the highest sensory neuron. Sensory impulses, therefore, stream to the pallium by the highest sensory neuron as well as to the thalamus by the second sensory neuron. How then does the pallium stand in relation to the thalamus in the functional rôle as a sensory receptor. In dealing with the corpus striatum we shall see that there are good reasons for believing that it was, in the typical mammalian brain, the great seat of the ordering of movement; but that in certain well-defined directions its function has been usurped by the pallium in man. The same conditions appear to hold good for the thalamus—the great, typical mammalian, sensory receptor. There appear to be some elements of sensation that are usurped by the pallial area of the post-central region—some elements for which the highest sensory neuron, terminating in a cortical cell, seems to be the dominant agent.

These things are made more clear by a study of pathological conditions in man. If a man suffers from an apoplectic stroke, which results in what is called a *hemiplegia*, he evinces the condition of a paralysis affecting one side of his body. This effect is brought about by the interruption of the neuraxons passing downwards from the "motor" cortex: but with the interruption of these motor fibres there is also a damage to the upstreaming highest sensory neuraxons passing to the sensory cortex. A typical hemiplegia produces an interruption of the upper motor and the highest sensory neuraxons. A human being who has suffered damage in the "sensory" area of the post-central region of the cortex, or who has had the fibres of the highest sensory neurons interrupted in their course to the cortex, does not become anaesthetic upon the opposite side of the body, though he is paralyzed on that side. Although the motor functions are disturbed, manifesting that type of paralysis known as *upper motor neuron paralysis*, the sensory function is still retained as far as certain elements of sensation are concerned. The destruction of the sensory cortex, or of the highest sensory neuraxon, does not deprive the patient of feeling or sensation upon the affected side of the body. He can appreciate pain, heat, and cold; and stimuli of contact are felt in the normal way. He can appreciate the more crude, more violent, more affective and unaesthetic, undiscriminative elements of sensation. He knows pleasure from pain, he knows comfort from discomfort of contact, but he has no discrimination of contact. Spatial discrimination is lacking: he has lost the components of his stereognostic sense. He cannot isolate or localize separate contacts made simultaneously. He cannot judge of graduated contacts. He is unable to judge of the increments of weights when placed upon the palm of his hand when his hand is unsupported, and he cannot judge increments of pressure when his hand is supported by resting upon a table. He cannot appreciate and realize the likeness or unlikeness of objects brought into contact with his sensory surfaces. Moreover, he cannot determine the spatial relations of objects touched: he fails to appreciate their innate attributes and so lacks the realization of the form, consistency and density of objects that he handles. All these losses apply to objective sensation—the spatial relations, the complex properties, the discriminative aesthetic characters of objects touched and handled.

As for subjective sensation, the loss is the same; the patient fails to appreciate the position in space of his limbs or the parts of his limbs. For our own bodies, as for objects outside our bodies, the cortex is the receptor of those discriminative sensory stimuli that subserve so largely the appreciation of spatial relations.

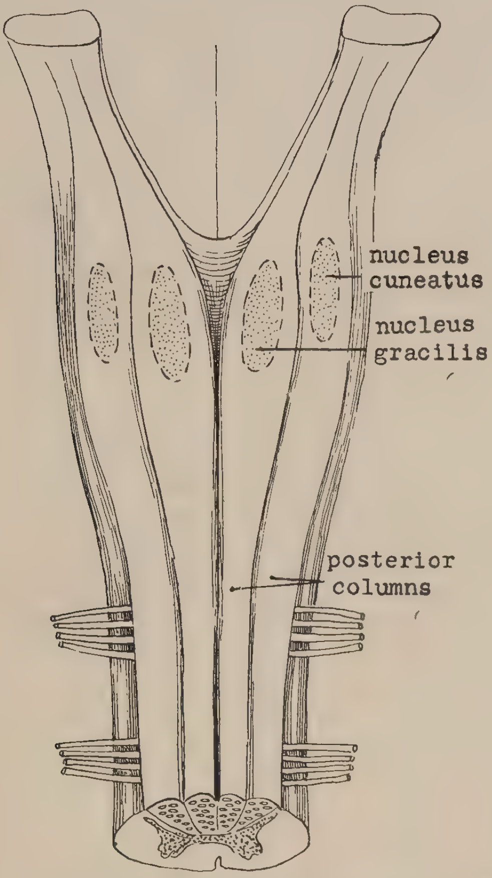


Figure 48.—Posterior (dorsal) aspect of the upper extremity of the spinal cord.

The highest sensory neuron, therefore, does not deal with what has been termed "feeling tone" but with the discriminative aspects of sensation, and it would seem that in the regrouping of the fibres in the spinal cord there has been achieved a separation by which the lowest sensory neuraxons, which run the longest course in the spinal cord and whose short second neuraxons cross in the decussation of the fillet, were most definitely destined to force their way to the level of the cortex.

Regarded in this way, we may say that the posterior columns of the spinal cord, containing the longest lower sensory neuraxons, the nuclei gracilis and cuneatus, and the decussating fibres of the fillet, constitute an entity of the conducting system of sensory impulses. This entity conveys to the cortex those impulses especially related to the spatial and discriminative realization of outside objects and of parts of our own body. Conversely we may say that those lowest sensory neuraxons, which effect their termination almost immediately and so give way to the second sensory neuraxon in the lateral column of the opposite side of the cord, are more definitely thalamic in representaton. The thalamus deals with stimuli capable of producing sensations of a change in state: it deals with feeling tone, and with stimuli having a highly-coloured affective quality. The sooner the crossing of the second neuraxon, the more crudely affective is the nature of the impulse carried, and the more definite its thalamic representation. The later the crossing, the more spatially discriminative is the quality of the impulse, and the more definite the pallial representation. Here, then, there is a reappearance of the great main factors of sensibility, for although the qualities of epicritic and protopathic are lost at the first sensory synapse, and are not revealed in lesions of the spinal cord, they manifest themselves again in their essential nature in the ultimate grouping in the brain. The thalamus is evidently the great, primitive, cerebral sensory receptor for primitive or protopathic sensory stimuli. It is the highest centre for the crude, protopathic, affective, unaesthetic, undiscriminative components of feeling tone. The pallial area of the so-called "sensory" cortex is the receptor for the super-added discriminative, spatial components, which, in their essential nature, are the epicritic factors of common sensibility.

Just as in the lowest sensory neuron we have seen that the epicritic element is something derived from and added to the protopathic element, so in the terminal cerebral receptors the same thing is true. The pallial element is something added to, something derived from and overlying and controlling the cruder, more highly coloured, affective, constituents of the thalamic element.

CHAPTER XX

THE THALAMUS AND SENSATION

The thalamus is an ancient heritage, for it constitutes with the striatum that primitive thalamo-striate complex which is the first vertebrate correlation executive system, precursor of those changes which begot the pallium. The primitive thalamus is developed in intimate association with the olfactory and gustatory centres of the primitive brain and there would seem to be no doubt that its initial function is that of the correlating of olfactory and gustatory stimuli with the executive mechanism for producing those movements essential to the business of ingesting food. But it is not long before this primitive basal thalamus enlarges its activities and its anatomical connections: it becomes a correlation centre for more widespread stimuli than those that are mainly concerned with food-getting. It becomes a general somatic stimulus correlator and expresses this enlargement of its powers in the development of those added parts which may be termed in general as the neo-thalamus.

In man the thalamus is a large and important nuclear mass (see Figure 49); and moreover it is one that has not lost its primitive function as a great sensory head station; it has merely had this function overlaid, controlled, and in a measure subdued by the development of the pallium. In Chapter XIX we have dismissed the functions of the human thalamus by saying that it is the nuclear mass that deals with feeling tone and with stimuli having a highly coloured affective quality. But it is necessary to define these functions more precisely and fortunately the researches of Head and Gordon Holmes upon clinical cases of thalamic lesions makes this analysis a comparatively simple matter. It is obvious that in cases in which some lesion occurs in the immediate neighbourhood of the thalamus a variety of conditions might be produced, since the damage might fall on the pathways of the second sensory neuron going to the thalamic cells, on the thalamic cells themselves, on the highest sensory neurons passing from the thalamus to the cortex; or most likely it will affect all three entities. The lesion may, therefore, produce effects depending upon the removal of cortical influence as well as those depending upon the removal of thalamic influence. The separation of these two elements in the symptoms manifested in an actual case is not to-day a matter of great difficulty and we may say that when cortical influences are removed the patient will lack those discriminative elements of sensation which we have already considered; but he will also manifest alterations in sensation which are truly thalamic and which are due to the loss of the pallial repressive action on thalamic activity. When the cortical influence is removed the thalamus is released from the pallial overlordship and its real functions are shown in their true light. These real functions constitute that curious train of symp-

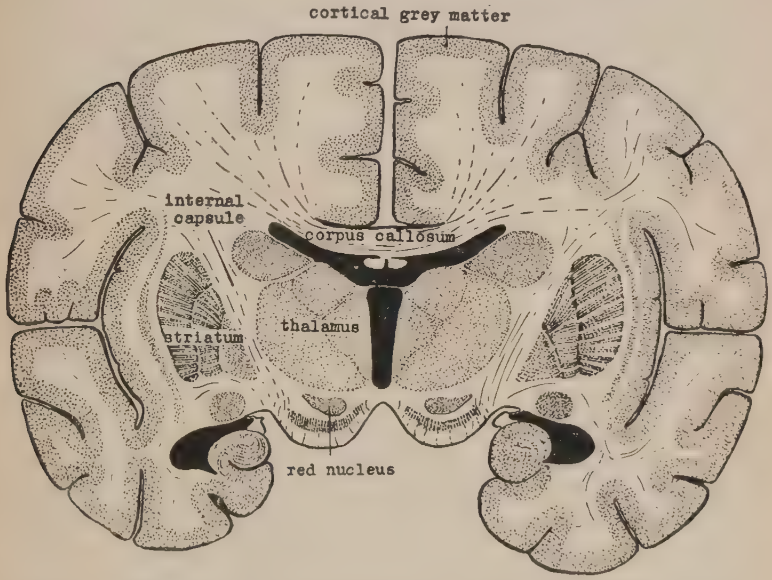


Figure 49.—Vertical, coronal, section through the human brain. The ventricular cavities are indicated in black.

toms which has been termed by Roussy the *syndrome thalamique*.

When, owing to some lesion, the thalamus becomes released, the changes in sensation are naturally manifested upon the opposite side of the body and both objectively and subjectively these changes are of a very remarkable character. We may say that in response to any stimulus that may be termed unpleasant the patient shows a remarkably exaggerated reaction. There is a condition of *hyperalgesia*, but this hyperalgesia does not necessarily mean that the patient is hypersensitive to pain, but that a painful stimulus produces a feeling of intolerable unpleasantness. The prick of a needle may not be so readily appreciated on the affected side as it is on the normal side of the body; even when it is appreciated the stimulus may not feel so distinctly sharp, but though it is less distinct it is far more unpleasantly painful. There may, therefore, be a lowered sensitiveness to the prick of a needle, but when the point is felt it produces an effect quite disproportionate with the intensity of the stimulus. Moreover the sensation felt is a distressing and unbearable discomfort rather than the sharp pain of the prick of a needle and it is not felt precisely at the spot stimulated but tends to produce an unpleasant sensation over a wide area. It is the same with other stimuli. If pressure is exerted upon a part where sensation is normal, the feeling of pressure, at first not unpleasant, will gradually become more and more disagreeable as the pressure is increased. On an affected part the pressure is less appreciated until it proceeds to the point at which it produces discomfort and then, almost explosively, the unpleasantness of the sensation becomes exaggerated so that it becomes intolerable. With stimuli of heat and cold, there is no greater appreciation of the stimuli upon the affected side, but when heat and cold are increased to the point of producing discomfort heat feels hotter and cold feels colder than it does upon the normal side of the body. If the skin of the affected parts be scraped or stroked or scratched or tickled, the result produced is the same; the stimulus is not more readily appreciated but if it is increased in intensity until it may be interpreted as being unpleasant it will suddenly flood the patient with a disagreeable and somewhat undefined sensation of distressing discomfort.

Thalamic over-action may produce some curious manifestations of this phenomenon of hyperalgesia. Patients will grow beards, since the feeling of a razor passing over the skin of the affected side of the face becomes unbearable as it seems as though it were being dragged across a raw surface. Even objection may be made to having the hair cut on the affected side of the head, and trimming the nails of the affected hand produces intolerable pain.

But we have seen that the thalamus is concerned with feeling tone generally and not only with the effective element of unpleasantness or discomfort. If in thalamic release the unpleasant is appreciated as intensely disagreeable, the pleasant should be interpreted as extremely pleasing. In the ordinary routine of testing sensation there are few stimuli applied that have any element of the pleasurable in them; nevertheless, the contact with things that are of a certain warmth excites in areas of normal sensibility a feeling of agreeable comfort. In cases of thalamic release this feeling too is exaggerated. The warmth of the touch of the hand may be exceedingly agreeable upon the affected side of the body. A hot water bottle may give great pleasure and this strangely enough even when the patient has lost all appreciation of thermal sensations over the affected area. To the normal side of the body the hot water bottle feels warm: on the affected side of the body it produces no sensation of warmth or heat but it feels extremely nice and comfortable. Moreover this feeling is not limited to the area in contact with the hot water bottle:—it makes the patient feel "nice all over." Although the sensation of pleasurable warmth is a very striking feature in these cases, it is a noteworthy fact that in the series of patients examined by Head and Gordon Holmes there was no evidence that such a thing as a sensation of pleasurable cold exists.

More remarkable still are the psychic and emotional manifestations of thalamic over-action. The two sides of the body determine two sides of the world for the individual, and one side of the body is affected by thalamic release. Music is often associated with strange diffuse feelings of bodily discomfort. To hear music is often to beget an emotional state of distress in the affected side of the body. Intense pain, ill defined but intolerable and spreading all over the affected side, may make it impossible for a patient with a real love of music to listen to the simplest performance. If the musical note be produced by a tuning fork so that its effect may be tested upon the two sides of the body, the patient will at once declare that the sound is only objectionable and only produces the pains when it is heard through the ear of the affected side. The sound of a choir singing may be pleasant enough when it comes from one side, but it may be intolerable when it proceeds from the other. This divided emotional outlook upon the world is also manifested in the intense dislike which some patients affected with over-action of the thalamus have for anyone to sit upon their affected side and this dislike results not from fear that their neighbour will touch and hurt them, but from an ill-defined dislike of a situation which produces a feeling of discomfort on the affected side. In such cases an uncomfortable feeling is developed towards a person situated upon the affected side: but the opposite condition is also produced and the patient may feel more kindly disposed towards a normally pleasant presence when this occupies a position on the affected side. Even patients have discovered that since one half of the body is more responsive to pleasant as well as to unpleasant stimuli, they may feel more than normally amorous with that side of the body. A patient has noticed that he seemed to "crave for sympathy on his right side." Indeed, as Head reports, he confessed, "I crave to place my right hand on the soft skin of a woman. It's my right hand that wants the consolation." It would seem to be possible that one might be very much in love only when the object of one's affections were situated upon either the right hand or the left.

As for subjective sensations their description is always vague and their type is protean; only one thing they have in common and that is that they are always extremely disagreeable and are but indefinitely localized. So strange are the descriptive terms used by those who suffer from them, and so difficult is their description, that there is always a danger that the observer may mistake them for being no more than the manifestations of hysteria. Equally strange are the devices adopted by the sufferer for alleviating the distressing feelings. One must always wear a glove upon the affected hand, and another cannot attend divine service unless he wears his hat, since music produces intolerable discomfort on one side of his body. It is probable that thalamic release occurs quite apart from gross lesions of the thalamo-cortical pathway: and this not only in the mild conditions under which highly coloured affective feeling runs temporary riot. It is possible that there is a thalamic element in certain cases of facial neuralgia—and extremely probable that in the curious condition known as *causalgia* thalamic release and not peripheral nerve involvement is the cause of the strange assemblage of symptoms. We have subdued the thalamus by giving the pallium the overlordship, but we have not conquered it.

CHAPTER XXI

INFORMATIVE AREAS

The thalamus we may say deals with generalities of sensation: the cortex is concerned with specialities. For the thalamus it may be enough that it is informed that some external object is touching the surface of the body: for the cortex there must be the added knowledge as to exactly what part of the body is touched and what exactly is the nature of the object that has made the contact. It is obvious that different parts of our body tell of these things in very different measure. Even with my eyes shut I may know more of some object touched by my lips that I can learn if the object makes contact with the middle of my back. Though blind I may still know far more if it is my hands that make the contact and perform the examination. But it is when my eyes are used in conjunction with my hands that I gain that tactile knowledge that is so definitely pallial in its nature. A whole train of coincident changes are involved in the completed human mechanism of the manual examination of objects carried out under the supervision of the eyes. The eyes must be co-ordinately moved and focussed, a point of precise acuity of vision must be developed. For the full perfection of the process we must have binocular and bimacular stereoscopic vision: and we must have fine, skilled, movements of digits whose sensitive surface is not dulled by their being employed as mere instruments of support and progression.

This is what evolution has meant for the human brain. It has had evolved a mechanism of hand and eye: a mechanism which by its very nature makes possible that tactile knowledge that is so essentially the educative factor of the pallial element in sensation. There has been a harmonious development of these things: and it is one of the great assets of our stock that no one element in the sequence was selected for undue specialization: the changes in hand and eye and brain have been co-ordinated into a harmonious growth. We have not overdone the eye development as *Tarsius* has; we have not unduly emphasized the hand as has *Chiromys*.

In this evolution there is unfolded that whole story of the arboreal apprenticeship of the human stock. It was life among the branches that liberated the hand from the servile business of supporting the body weight and set it free to grasp strange objects, to feel them, examine them, weigh them and turn them this way and that so that all aspects could be seen and correlated. It was the liberated hand that carried food to the mouth and so permitted that shortening of the muzzle that was the necessary precursor of the changes in the eyes. The shortened muzzle created that change by which lateral eyes were brought to the front of the face, and so permitted the development of binocular and stereoscopic vision and conjugate movements of the two eyes. It was the hands which, by holding objects at near range for ocular examination, produced a point of precise vision and led to the development of a binocular fixation field and the perfection of bimacular vision.

What was learned by touch before these changes had taken place was as nothing when compared with the knowledge acquired by the simple act of an arboreal member of our phylum when the first strange fruit was plucked and examined with minute attention by the hand guided by the scrutiny of the eyes. It was now that the discriminative elements of sensation streamed to the brain: the surface texture, the low grades of temperature, consistence, weight, density, precise contour and spatial relations of objects could all be appreciated and epicritic or cortical sensation replaced the mere vague sensation of contact with an outside body.

As the sensory informer that can add the discriminative qualities of sensation, the hand, used harmoniously with the eyes, is still paramount. Nevertheless, there are other sensory informers besides the hand. From the point of view of common cutaneous sensation we learn most of the outside world by the hand: but in our phylogenetic story we have had other important sensory informers. The primitive tactile snout area, subserved by the great trigeminal nerve, has served its turn and still is the great tactile informer of lower mammals. In us the great sensitiveness of the skin of the lips and face is well known. And it is a curious reflection that in sampling our fellows we may rub noses or kiss, depending on our race, or we may employ our next phylogenetic sensory informer and merely shake hands. The great trigeminal nerve, the nerve of the tactile snout, has certain peculiarities, and in some measure these peculiarities are shared by the median, the nerve of the tactile informative hand, and by the internal popliteal, the nerve of the tactile informative sole of the foot. From the hand we learn almost all, but from the foot we learn much, since by the sole of the foot we maintain contact between ourselves and the outside world. It is by the sole of the foot that we maintain tactile contact with our environment during the great part of our waking lives. It is by the soles of the feet that blind men learn much in their walks abroad: and it is only those who have suffered a diminution of the sensitiveness of the sole who can realize the vast importance of this informative area. Though it may be separated from contact with outside things by a sock and a thick piece of leather, the sole of the foot is still all important as an informative area which tells us of our environment. When we stand up, or walk about, we maintain tactile contact with our surroundings by the soles of the feet, but when we sit down it is the ischial region that keeps us in sensory contact with our surroundings. Herein, probably, lies the explanation of the curious naked ischial region of some of the monkeys: it is by their naked ischial region that monkeys retain tactile contact with the branches on which they sit, whilst their hands and feet are otherwise employed. Though they may afterwards be employed as secondary sexual adornments—as walls of houses are used as areas for adfixing glaring advertisements—nevertheless their primary function is almost certainly tactile. Even in man there is a curious informative sensitiveness of this region. When in deep-sea cable work, the grapnel is trailed over the ocean bed to grasp the cable, lying maybe more than two miles below the surface, it is important to know when the grapnel has encountered the cable. The grapnel rope passes from the bows of the ship, running over a fixed wheel and under a wheel that is free to move up and down a vertical scale. When tension on the grapnel rope increases, the wheel rises, and by reading this dynamometer scale the officer knows when the cable has been grasped. But experienced officers do not rely upon the dynamometer, they sit on the grapnel rope, and when the grapnel, two miles below, encounters the cable, the strain upon the rope is appreciated more readily by the nerves of the ischial region than it is by the dynamometer.

To the philosopher, the fact that we rub noses, kiss, or shake hands with our fellows in order to learn of them, may open up a subject of some interest: but there is another interesting point we may recommend to the philosopher. We learn through certain definite sensory areas,—through these areas we also attempt to teach others. We chastise youth in the informative area of the hand or the informative ischial region—we have outgrown the simple method of smacking the face. We neglect the sole of the foot as a sensory teaching area, but it has by no means been neglected by the Turk.

CHAPTER XXII

THE PALLIUM AND AWARENESS

So far as the pallium is concerned with outside objects we have seen that the sensory functions are shown in the discriminative appreciation of the innate qualities and spatial relations of extraneous things. The objective sensory functions of the so-called sensory cortex are manifest in the realization of the discriminative, spatial and aesthetic elements of stimuli resulting from actual contact with the environment. But the pallium, in its sensory functions, has a still more important rôle on the subjective side. Stimuli may come to the pallium from the environment: they may also come from the body itself. By touching an object I may learn about the object: but in the contact I may also learn about myself. As I walk along I may go with my hands before me, at my sides, or behind my back. If my hands are before me or at my sides I may see them with my eyes and know where they are and what they are doing. But here is the curious feature of this simple happening: if they are behind my back and I cannot see them, I still know where they are and what they are doing. And this knowledge is detailed, and descends to minute particulars. I know the degree of bending of all my fingers; I know if my thumb is bent into my palm or held aloof; I know which hand is before and which behind; I know every detail of the position of every part of my fingers, wrists or forearms, though they are quite invisible.

Even if we limit our inquiry to the case of our hands behind our back we encounter a mystery. My hand held before my face and examined minutely by my eyes is in little better case than my hand held behind my back. I know what every joint and every part of it is doing, even if I can learn nothing of it by the aid of my eyes, or the touch of my other hand. I know of my hand as a part of my body projected in space and realize the relation of every joint and part of it as an entity which has a spatial projection.

Inside me, in the depths of my body, are parts capable of being moved by muscles, capable of being altered in their position in space and of being contracted, relaxed or expanded. These parts I cannot see: but neither can I see my hand behind my back. There is this difference, however—of my hand I know all, of my internal parts I know nothing. I have a picture of my hand as part of me projected in space, but of my stomach I have no picture. I do not know that it is a part of me and I do not know what its relations in space may be.

There is a great difference, therefore, between my hand and my stomach, of the one I know, of the other I know not, the position it occupies in space.

It becomes logical, therefore, to examine how this knowledge comes in the one case and not in the other and to make inquiry as to what part of the brain is concerned in the matter. How does this knowledge come? How do I know of myself? and what structures have part in the attainment of this knowledge? We have already seen how great a stride was made when detailed examination of objects held in the hands could be carried out by the eyes. A member of the Primates may conduct a thorough examination of a fruit or an insect held in its hand. It may know all about an external object from repeated examination. By the same process it may learn all about its hands as part of itself projected in space. Just as digital examination, when carried on under the scrutiny of the eye, may teach all about the innate properties and the spatial relations of the object examined, so may the hands be examined as objects of curiosity and they and their spatial relations become familiar in the process. The business may go further than this and the animal may learn of all parts of its body that can be examined with its eyes: it may realize its body as an entity projected in space.

To supplement all this the mobile, inquisitive hand may learn still more, for parts of the body that the animal cannot see may yet be felt with its hand, and so between visual and tactile channels its realization of the spatial relations, the contour and innate characters of a very large part of its body may be very complete.

In the case of man this knowledge may be increased.

I know of my body by my eyes. Every part of my external anatomy which I can see and examine with my eyes is familiar to me. I may know as much of my fleshy form as a monkey knows of itself by visual and digital examination, and I may know more, since I possess a mirror. Given the use of my eyes and aided by my mirror there are not many parts of my body with which I am not familiar. I have seen them, I have learned to know them, and I can picture them, even when my eyes are shut, as parts of my integral whole projected in space. Again I know of my body by examining it with my hand as a monkey knows of itself by digital examination: I know of my body from the feel of those parts I cannot see. I do not suppose I have ever seen my shoulder blades, but I know all about them since I have often felt them. Had I no mirror I should still know of my nose by reason of having felt it with my fingers.

Now what I know of my body is just what I have learned by touch and by vision. Of those parts of my body which I cannot touch and cannot see I know nothing. I may dissect cadavera, I may see coloured illustrations in books, I may be familiar with X-ray pictures, but in the end I cannot claim that I know my own stomach. I cannot pretend to be familiar with the doings and the spatial relations of my own ileo-caecal sphincter.

My hand behind my back is, therefore, in very different case from my stomach in my abdominal cavity. The one I know as a part of myself occupying a definite position in space, of the other I am unaware as an entity having spatial relations.

The contrast here is between a limb with its joints and muscles, and a mobile muscular viscus hidden from sight and touch in the abdominal cavity, and such a contrast has to be made in the case of man, for we may say that it is only his internal viscera of which he is unaware as spatial entities. But with the lower animals matters are very different. What does an elephant know of its hind legs from sight or touch? A very little reflection will convince us that our knowledge of the spatial relations of our limbs and external parts is far more complete than is that of most of the common mammals. We know of ourselves far more completely than any other animal does. Moreover in us it is evident from many commonplace facts of pathology that we know far more of our hands and arms than we do of our feet and legs: and the same is the case with the monkeys and probably with all mammals. To this subject we will return; but in the meanwhile there is the third question to answer, "What part of the brain is concerned in the attainment of this knowledge?"

Here we are not in doubt. Our knowledge of ourselves, our awareness of our parts and members, our realization of the spatial relations and the intimate details of the parts of our bodies, is a function of the pallium—it is the, so-called, sensory cortex of the post-central area that is concerned in this matter.

CHAPTER XXIII

THE ACQUIREMENT OF AWARENESS

We have seen in Chapter XIII that in the primitive mammal there was a precursor to the hand as a tactile examining organ. Before the hand was liberated from its duties of support and was freed for the office there was the sensitive nose and the muzzle region. The hand teaches us of the outside world, it also teaches us of itself and of the rest of the body. The muzzle region discharged these offices first, and first demanded a pallial rerepresentation.

In the primitive mammal the sensitive snout, with its tactile mystical vibrissae, and the face and jaws, with their separate sets of sensory hairs, are the parts of which the animal first gains knowledge, in the sense in which we are using the term knowledge (see Figure 50).

As has been pointed out by Elliot Smith, it was probably the overdoing of this sensory snout and clinging to its first achievement that arrested the progress of the archaic monotreme. The primitive mammal gained information through its great trigeminal nerve area, the advancing mammal progressed from this, but the Platypus elaborated and became a slave to its first achievement; it made a sensitive beak to the confusion of zoologists and to the arresting of its own progress. The Platypus made a graven image of its sensitive snout, Tarsius fell a victim of its own great triumph and remains a slave to its dominant eyes. It was the muzzle region that first gave information of the outside world. It was the muzzle region that first gave information of itself. The primitive mammal became aware of the muzzle region as a part of its body occupying a definite position in space. In the developing pallium of the primitive mammal the muzzle region—all that area beset with the sensory vibrissae—demands a place; a place in which we may say, crudely, is lodged a realization or an awareness of the muzzle as a part of the body occupying a definite projection in space. Here was a gain in brain building, for a new function had been added to the powers of the pallium and though sensory vibrissae might be elaborated, though sensory appendages of the most curious type may be added to the face, and though a sensory beak may absorb the informative activities of a Platypus, nevertheless, other mammalian stocks employed new channels for adding to their pallial achievements.

In the arboreal stock that produced the phylum of the Primates it was the hand, liberated from the servile function of supporting the body weight, that served as the new channel for acquiring knowledge. The animal learned of outside objects by the combined use of its eyes and its hands. By the same method it learned of its hand itself. It came to have a realization of its hand as a part of its body projected in space.

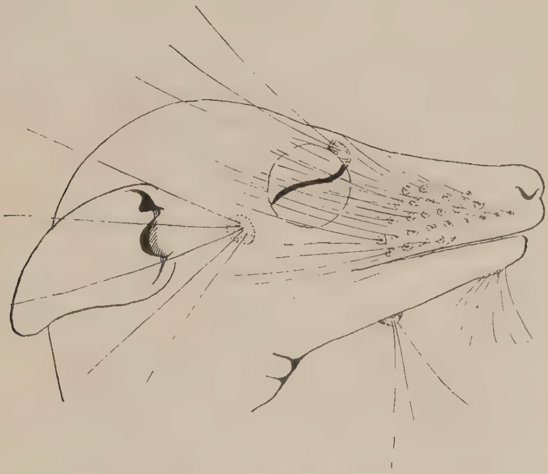


FIGURE 50.—The sensory vibrissae of the muzzle region of a typical lower mammal represented by the Australian Opossum (*Trichosurus*).

Even of its hand there was specialization, for the examining digits of its hand were mainly the thumb and index digits. Each digit has its office exalted or lowly, and the nomenclature employed by the old anatomists gave expression to this functional specialization. He who would probe his ear will still employ the digit named auricularis. It was of these digits that the arboreal animal gained a pallial knowledge as parts projected in space, and we may say that after the trigeminal nerve area it was the median nerve area of which the developing Primate became cortically aware. After the median nerve area of the two inner digits, the whole hand is known and realized by the process of examination and testing. The knowledge spreads; the animal knows of its wrists and forearms, its arms and shoulders, its trunk, thighs, legs and feet. It learns of itself: it comes to realize its body as an entity composed of parts projected in space as it examines them with hand and eye in the same way that it comes to a realization of the spatial relations of an external object. Its last gained knowledge will be that of the parts not visible, but still palpable, and so only partly known. Now, it is easy enough to picture this progress of the gain of an awareness of the parts of the body projected in space; it seems very simple from observations upon living members of the Primates to deduce an order in which this realization came to the pallium.

Nevertheless this apparent order will have to stand the test of experimental investigation.

One of the most important pallial fields is that which is often termed the "sensory area," or more broadly, the "kinaesthetic area" from its supposed function, or post-central area from its anatomical site behind the central sulcus of the cortex.

It is this pallial area that is concerned with what we have attempted to express as the realization or awareness of the parts of the body as entities projected in space. This cortical field is one which has, maybe, suffered somewhat from experimental investigations carried out upon lower animals. It is not a field that is concerned with sensation, in the sense in which we ordinarily use the word sensation, and we may defend here the thesis that, from the subjective side, it deals with the spatial realization of parts of our own bodies. Whatever be the quality with which this pallial area is concerned there is no doubt as to the order of rerepresentation in the area. This has been determined both by pathological studies on man and by experiments on animals. In the oldest part of the area, which is in continuity with the basal ganglia, is the area for the lips, mouth and face. The old muzzle region has first place in this developing pallial area. Next in order (and above in anatomical situation) we might look to find the remaining parts of the body in anatomical sequence: but this expectation is not fulfilled. We do not find the shoulders, the arm, the elbows, the forearm, the wrist, hand and fingers represented in that order; for the whole rerepresentation is reversed. Next to the great muzzle region is the thumb and index finger, then the other parts of the hand, the wrist, the forearm and so to the shoulder and the trunk. *The arm is reversed in rerepresentation, but the leg is rerepresented in its anatomical sequence*, for when the area for the trunk is passed we come to the areas for the hip, thigh, knee, leg and ankle and foot in anatomical order (see Figure 51).

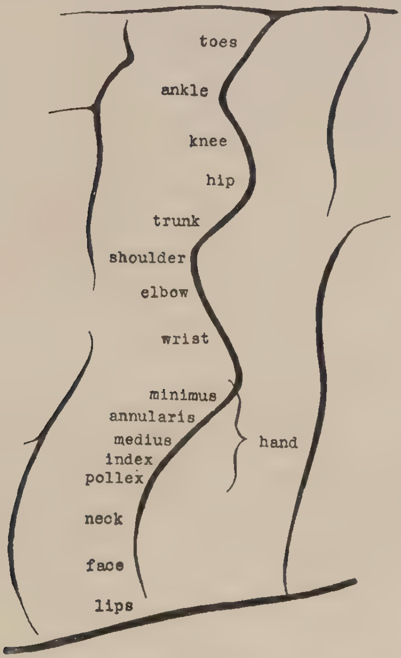


FIGURE 51.—Diagram of the sulcus centralis and the order of rerepresentation of parts of the body in the cortex.

Last in rerepresentation in the human cortex is the area of the perineum.

The order of the rerepresentation in the so-called sensory area is well known and yet its apparent topsy-turvy nature does not appear to have excited the attention it deserves. If the parts of the body are to receive pallial rerepresentation surely it is a remarkable thing that the arm should be, anatomically, turned upside down. It is remarkable that the thumb should be next to the muzzle.

If rerepresentation of the body needed place in the pallium it would be natural to imagine it carried out a definite anatomical sequence. The fact that this sequence is not adhered to, and that the order is strangely irregular, and moreover coincides with what we have pictured as the order of the acquirement of knowledge is surely an arresting finding.

We have imagined the knowledge of the body passing from the muzzle to the hand. We have pictured the knowledge of the body acquired by the examining inquisitive hand carried out under the inspection of the eyes.

In the human brain we have only to note the order of the actual rerepresentation of the body and to observe how it marches with the development of the visual pallial area to be convinced that we have learned of ourselves from the muzzle to the hand and from the hand and the eyes to the rest of the body. As the last attainment of knowledge of ourselves there seems to be the area of the perineum and, judging from clinical findings, it would seem that here the pallial knowledge was far from complete.

CHAPTER XXIV

THE PALLIUM AND THE BODY

In the post-central area of the cerebral cortex our realization of our bodies, and our realization of other objects of which we can discriminate the spatial relations, are lodged in a wider field than that usually determined as the "sensory" region. The war taught much concerning these things. Cortical wounds extending over an area from the central sulcus to the angular gyrus produce a loss of this factor of "sensation": the loss of spatial realization.

Although in experimental work carried out upon animals a more or less equal share of the sensory cortical area appears to be allotted to each member, and the hand, arm, leg and foot, for instance, appear to be of comparable importance, in the human brain the apportioning of areas to members is remarkably unequal.

There is rank in rerepresentation; and the human hand and foot take precedence. In the hand "each digit is a unit, which can be used in an isolated act either of motion or sensation; as such it is represented topographically in the cortex" (Head). More than this, if a cortical injury of the post-central area affects the face it will likely involve the thumb; and if it involves the foot it will likely cause disturbance in the spatial appreciations of the little finger.

The hand occupies the great mid region of the sensory area and it is spread large over this area with the thumb downwards towards the face and the little finger upwards towards the foot. The body is rerepresented in the sensory area not as an anatomical thing but as parts which are capable of undergoing "conscious changes in function" (Head) and among these parts the hand is dominant.

Now, if we are correct in assuming that in this area is lodged an awareness of parts of the body which are capable of undergoing conscious changes, and of which the spatial relations are known, it is easy to see that, regarding only this aspect of what is termed "sensation" there are great possibilities for the display of the heightening and lowering of the functions of this cortical field.

I know of my hand held behind my back, I realize that on my hand there are certain separate digits. I am aware of the parts of my body of which I realize the spatial relations: but this knowledge is not irksome. I am merely in a neutral state of being aware of my parts. When I lie down to sleep I am still aware of the disposition of my limbs, but the realization passes as sleep comes on. So much of the sensory knowledge of my body is present: enough to enable me to dispose it in ordered fashion, but no more than that: the knowledge is no burden to me. But, even if I have no pain or any other abnormal sensation in any part of my body, my knowledge may become burdensome. The realization of my body may not fade when I wish to sleep. To everyone it has happened that the obtrusive awareness of his limbs has become a burden that has kept sleep away. When I am awake and not engaged in any active occupation my consciousness is undisturbed by my knowledge of the spatial relations of the external parts of my body just as it remains unaware of the precise position of my viscera. In the one case I know of the disposition of my members, but the knowledge is not obtrusive, in the other case I have no knowledge. As I sit in idleness I know that my legs are crossed, but unless the position produces some discomfort, this knowledge is not insistent in its demands for recognition. As my hand lies idle I am well aware that I have digits attached to it; but I have not an awareness of five individual digits when in a state of complete passiveness. My thumb is more or less aloof from my other digits and even in the most neutral of circumstances I am aware of its individuality: the index finger is in like case; but of the middle, ring, and little fingers, my knowledge is less defined if I allow my hand to remain in complete idleness. Should I wish to count my fingers, unaided by my eyes, when my hand lies entirely passive, I shall probably encounter difficulty. I shall be tempted to move each one in turn in order to establish its individuality. But in the case of the thumb this is unnecessary, my thumb is established as an individual in my consciousness and so too, but to a rather lesser degree, is my index finger. With my foot the case is very different. Were I unable to see my toes and unable to examine them with my fingers, I should not know how many pedal digits I possessed, nor even should I be certain that I had any separate digits with the exception of my big toe. Moreover I cannot establish the individual identity of my four outer toes by differential movements carried on within my socks and boots. Cortically I am unaware of my individual toes, though from sight and touch I know that I possess them. But these things are capable of alteration. A cortical awareness of the individuality of toes may become irksome. For those who only realize that their boots lodge feet with big toes and an undefinable huddle of other toes it is difficult to picture the condition of the irksome realization of the individuality of toes. Nevertheless these conditions are common enough, and it is well for the clinician to appreciate their significance as indications of heightened cortical realization.

From these apparently trivial manifestations of undue vividness of the realization of the parts of our bodies—manifestations that may be stigmatized as neurasthenic if you will—we may pass to a far grander display of cortical awareness.

We have all heard of the veteran, who, leaving his leg on some brave field, has for years felt his toes during the cold weather, despite the fact that his foot remained in the Crimea and he has no more than a stump and a wooden leg. Although he has a wooden leg he still feels his toes. That he does this is not by reason of heightened cortical awareness, but because the nerves which used to run to his toes are still in his stump and are subjected to irritation. The veteran probably has a stump neuroma: the nerves which used to run to his toes are involved in scar tissue in his stump, and being irritated there, send impulses upwards which are still interpreted as coming from the toes to which they used to run. If the neuroma is excised and the irritation removed from the cut end of the nerve, the sensations will cease, he will not feel his toes any more.

But there is a condition, which though somewhat like

LINACRE COLLEGE LIBRARY
UNIVERSITY OF OXFORD

that caused by a stump neuroma to casual examination, is a far graver thing and is a real and terrible manifestation of cortical awareness.

A man has a painful wound in, say, the hand. For a long while the arm remains intensely painful and the condition, going from bad to worse, calls at last for amputation. The part is amputated, say through the forearm, but the condition is not improved. The missing part of the arm is still there, still dinning its recognition into consciousness. Attention is turned to the stump, a neuroma is searched for, a higher amputation performed later. The arm is still there. More amputations may be done, all the sensory nerves may be cut, all the posterior roots of nerves of the arm divided. The arm is still there. It still demands almost exclusive recognition by day and keeps the patient awake by night. This is the condition of a *phantom limb*, different altogether from the case of the stump neuroma. A phantom limb is ever present as an entity projected in space, it does not tickle like the veteran's absent toes: it is a perpetual presence of a limb having spatial relations. It lies on the coverlet of the patient's bed and the hand opens and shuts. It may twist and turn about, bend and straighten out again and in all its doings it knows no control. It is a limb more real in its absence than any actual limb and one that goes far towards absorbing the whole of the patient's cortical activities. A phantom limb is the product of abnormal cortical awareness, the product of a cortex into which a real limb has almost indelibly dinned a terrible recognition of its presence.

Twenty operations will not remove, but rather tend to establish more permanently, the phantom: only by erasing from the cortex the dominant realization of the absent member can relief be obtained.

Just as the cortical awareness of the parts of the body may be rendered abnormally acute, so it may be dulled. A patient who has suffered injury to the post-central cortical area may complain that the affected member feels dull or dead, or numb, or as one of Head's patients expressed it, that "it hardly seems to count." The member has in fact a tendency to be lost to the consciousness as a part projected in space.

The affected hand "hardly seems to count": though still a useful member capable of performing its allotted rôle of muscular movements, it is not fully employed because it "hardly seems to count." It is a useful tool, but like a tool it is apt to be laid aside on the bench and forgotten; the cortical awareness of the member is so lowered that the patient may forget to use it as he may neglect a tool in his workshop.

Head's experiment on a man who had suffered a cortical wound involving his arm area demonstrates clearly how real is this loss of the appreciation of spatial relations. The patient's affected arm is laid on the coverlet of the bed and he is told to look at it and note the position in which it lies. Whilst he is looking at it, the hand is touched in several places and to these spots he is told to point with his unaffected hand. He now closes his eyes, and the affected arm is carefully removed from the coverlet and placed at right angles to its former position. The affected hand is again touched and the patient is asked to indicate the spot with his eyes still closed. He touches the coverlet on the place where the hand originally lay on the bed. When he shut his eyes he retained a visual image of his hand on the bed clothes: his visual cortex knew where the hand was, but his sensory cortex does not know where his hand now is. He, therefore, still points to his affected hand in the place in which he last had cortical knowledge of it.

In this case the patient has lost the knowledge of the spatial relations and the spatial existence of his arm because the cortical area in which this knowledge is stored is destroyed. But the knowledge may diminish without an actual loss of the cortical area by injury or disease. Just as the realization of a member may be heightened by the over-activity of the cortical area so it may be dimmed by the lowering of the activity of the area. It is probable that different individuals may vary widely in their normal awareness of parts of the body, and those who perform the most complex and most specialized and skilled movements with their separate fingers have a better realization of their digits than have those who use the hand only for gross or coarse actions in which the digits do not function as individual entities.

We would suppose that use might create a wider and more precise cortical realization. It is certain that disuse may beget a lowering of the cortical realization. An arm that is not a reality may dominate cortical awareness and become a phantom; an arm that is a reality may fade from cortical awareness and be reduced to a condition in which "it hardly seems to count." To this subject we will return in connection with the question of movement. Meanwhile it is worth inquiring a little further as to the manner in which the knowledge of our bodies is ordered. I know of my hand and of its separation from the forearm by the wrist. I know of my forearm and its separation from the arm by the elbow. I might almost say that I know of my members as segments or as "joints" into which I could readily be dismembered.

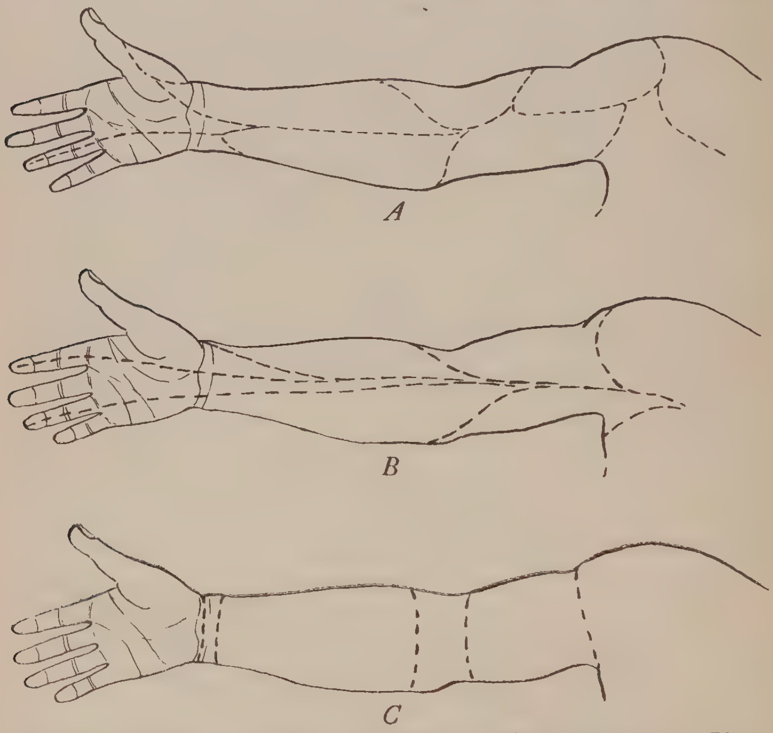


FIGURE 52.—The areas of the arm (A) as supplied by individual sensory nerves. (B) as supplied by segmental spinal cord sensory roots and (C) as they are apt to be known to the cortex.

Of these segments I have no very perfect correlation of back and front, unless the part be highly mobile as is the hand. Of my trunk the knowledge of the back is very slight and such as it is, it is not correlated with my knowledge of the front. Now this is of importance. The nerves that subserve the two functions of sensation and movement are not distributed to the body in this system of "joints." A cutaneous nerve, or a system of cutaneous nerves, will supply an area which comprises only one part of such a segment or a part of several segments (see Figure 52). A motor nerve, or a group of motor nerves, in the same way, will supply muscles unrelated to such a segment as is represented in my cortical knowledge of my body.

Our cortical awareness does not embrace a knowledge of the bodily areas to which separate nerve roots, or separate nerves, are supplied. It, therefore, happens that a paralysis or an anaesthesia if of cortical, or as it may be termed functional or hysterical, origin will tend to affect a segment, which is a subdivision of the body altogether different from the areas to which individual nerve roots, or individual nerves, are supplied for movement or sensation. The clinician knows at once, when a "glove area" anaesthesia or paralysis is the manifestation of nervous upset, that no nerve tract, root, trunk, or branch is involved, for the brain alone knows of a glove area and can picture its ability to feel or move.

CHAPTER XXV

THE PALLIUM AND MOVEMENT

As far as our own bodies are concerned, we have seen that what the sensory or post-central area of the cerebral cortex is concerned with is the awareness of the parts of our bodies as entities projected in space. So much seems definite when we are dealing with the so-called sensory area of the human cortex. If this is true of the sensory cortex, what of that which is named the motor, or pre-central, or pre-rolandic area of the cortex.

If I know the position of a part of my body as an entity projected in space, it seems likely that the so-called motor area might be the field in which there could be initiated an impulse to dictate an alteration of this position in space. And as a fact, every clinical finding appears to point to the conclusion that in man the alteration of the position in space of a part whose projection in space is realized, is the true function of the pre-rolandic, pre-central, or motor area of the cortex.

It will readily be seen that, should these generalizations be true, there must be two grades of motor activity. In the first, the position of the part is realized in the post-central cortex and its alteration is dictated by the pre-central cortex. In the second, the position of the part is not realized in the post-central cortex and the pre-central cortex has no jurisdiction over it. We could divide all parts and actions of the body into two categories. In the first would be those we know, and in the second those we do not know. The first group it seems likely we could regulate by what we term our will, initiated in the "motor" cortex. If we know of the disposition of a part, it seems reasonable to suppose we could will the alteration of its disposition. The second group—of which our cortex does not know the spatial relations—seems likely to be beyond our will. If we do not know what is the disposition of a part, how can we set about giving instructions for an alteration of its disposition? It seems that since these things are without the sphere of our awareness, they must be undertaken by something that is not our will.

I know where my fingers are, what they are doing, and I can will that they shall change their position. Even as an anatomist, I do not know exactly where the pyloric end of my stomach is, still less do I know what it is doing, and I cannot will that it shall do anything. Something else, something that is not known to me as I, must dictate the alterations that take place in the mobile pyloric end of my stomach. It is the actions that fall into these two categories that are known, crudely, as voluntary and involuntary movements.

A voluntary action consists in the willed alteration of the position of a part whose projection in space we realize. The alteration of the position of a part whose projection in space we do not realize is an involuntary action. Such a subdivision of action into voluntary and involuntary is of basal importance in the study of movement. Actions cannot be classified by the muscles which are called upon to perform them, nor can muscles be classified into voluntary and involuntary by their anatomical characters. All such classifications are misleading. The terms skeletal, striated or voluntary; and visceral, unstriated and involuntary cannot be used with any precision when an attempt is made to correlate the character and structure of muscles with the type of movements they perform.

The striated, skeletal or so-called voluntary muscles perform a wide series of actions which are involuntary and beyond the control of the will. The actions of sneezing, coughing, breathing and a host of others are performed by ordinary skeletal, striated muscles, but the initiation of these actions is not cortical or willed. We may say, in general terms, that striated muscles perform those actions in which rapidity and precision of movement are required, whilst unstriated muscles subserve those actions characterized by a leisurely, rhythmical and unprecise type of movement. For the most part, the precise and rapid actions are those of the parts of our bodies of which we appreciate the spatial relations and of which we can dictate an ordered alteration. To a great extent, therefore, these muscles perform actions to which we have given the name voluntary, but this nomenclature cannot rightly be extended to the muscles that perform the action. It is the action that is voluntary, not the muscles that perform the action.

Such a conclusion naturally follows from the consideration of such a simple involuntary action as sneezing; a complex action, which is performed with rapidity and precision by striated skeletal muscles, but yet which is itself a reflex initiated by centres below the cortical level. There is no voluntary muscle and no involuntary muscle in the strict usage of the terms. There are voluntary movements and involuntary movements, which differ solely in the site of the initiation of the impulse for the movement, but even in this case, definition is apt to give way when pushed to extremities. My respiratory movements are carried on waking or sleeping; a host of striated, skeletal muscles produces respiratory movements of the chest and abdomen in the complete absence of any volition. Nevertheless, I can dictate alterations of my respiratory movements. I can hold my breath, breathe deeply, breathe either with the abdomen or with the thorax, in a regulated and voluntary fashion. I can initiate respiratory movements from my motor cortex or I can allow them to be initiated by a lower sub-cortical centre. The action of coughing may be quite beyond our control—it may be purely reflex; yet when asked by a physician to cough during the progress of his examination, I can voluntarily rehearse all the movements that constitute an ordinary reflex cough. I can cough to order—when the action is cortical or voluntary; or I may cough in direct opposition to my wishes. A sneeze is typically a reflex, involuntary act, yet it is possible to produce a passable imitation of a sneeze by taking thought upon the matter. Even in applying the terms voluntary and involuntary to movements it is, therefore, obvious that we must not press the terminology to the breaking point of definition in all cases.

A consideration of the method by which we have pictured the motor cortex as coming into being, combined with the study of such an act as a reflex sneeze, makes the great axiom of cortical rerepresentation of movement —that *movements, not muscles, are represented in the cortex*— easy to understand.

I can appreciate the position of a part of my body projected in space. I can initiate a desired alteration of its position in space; but of the agents that carry out this alteration, I know nothing.

In general, I know no more of my muscles than I do of the pyloric end of my stomach.

What is lodged, therefore, in our motor, pre-central or pre-rolandic cortex is the power to dictate the alteration in space of a part the position in space of which is realized or known in the so-called sensory, post-central, or post-rolandic area of the cortex. We may, for convenience, adopt a handy, but somewhat inexact, terminology and say that in our motor cortex are lodged "action patterns" or "pictured movements." The motor cortex provides the physical basis for the initiation of those movements that we can realize and that we can see and feel ourselves doing.

CHAPTER XXVI

MOVEMENTS AND MUSCLES

More may be learned of the functions of the pre-central area of the pallium by the study of those cases in which injury of the area or of the pathways leading from it, have resulted in a cessation of its activities.

If the motor cortex be damaged, or if by interruption of the tracts leading from it, its influence cannot be exerted upon body movements there is produced that very definite type of paralysis known as *upper motor neuron paralysis*.

An apoplectic seizure or a "stroke" is the outward evidence of such an interruption and its consequence is *hemiplegia* or paralysis of one side of the body, and naturally, when interruption is cortical or capsular, of the side of the body opposite to that on which the damage has taken place. A case of hemiplegia furnishes the classical form of the condition of upper motor neuron paralysis.

In such a paralysis the muscles do not become as dead things: they still have the lower motor neuron intact and ready to hand on messages: but the message from the cortex does not pass. It is not a case of muscles that have abandoned all hope of receiving stimuli; indeed they may be said to live in constant expectation of the stimulus that is unable to reach them. Muscles deprived of the influence of the cortico-spinal impulses may be said to live on the alert, always waiting for the command, always ready to act. They do not lose their tone and become flaccid; rather their tone is increased and they become spastic in their functions. If the paralysis is of long duration this condition of the muscles may produce deformity, since the most powerful set of muscles will, by the increased tone of the mass, tend to bend the joints in the direction of their pull and so produce contractures.

Again such paralyzed muscles do not undergo degeneration; their reactions to electrical stimulation are not abolished or lessened and they will respond with equal alacrity to both faradic and galvanic currents. The ordinary reflexes and muscle and tendon jerks may be elicited from the muscles of the paralyzed part; response in such reflexes is not abolished but rather it is increased. But the muscles do more than retain such simple reflex powers, for they can take part in any movement for which the initiating level is below the cortex. Many muscles, as we have seen, can act both at the dictates of the cortex or in response to the impulses arising from some lower centre. They take part in what are termed voluntary actions as well as in involuntary actions. Since, in an interruption of the cortico-spinal tracts, it is only the cortical influence that is removed, it is easy to see that, although the voluntary action is impossible, nevertheless, a considerable range of involuntary actions may be left for the muscles to perform. It is for this reason that the curious clinical finding that *a muscle may be paralyzed for one movement and yet be free to act normally in another* is brought about. This condition is seen to perfection in the case of such muscles as pass from the shoulder girdle and the fore-limbs to the ribs. They may act from the ribs as a fixed point and so produce movements of the fore-limbs, or they may act from the fore-limbs or the shoulder girdle as their origin when their attachment to the rib becomes their insertion or moveable point. In such a case, a voluntary attempt to move the arm will produce no result, since the initiation of the movement involves the cortex and the cortico-spinal pathways. But should the patient sneeze, then all the muscles which previously showed complete paralysis will act in a normal manner and produce the rapid elevation of the ribs characteristic of this reflex act. Sneezing is a complicated muscular action which is produced as a reflex; it is not initiated from the cortex since it is carried out in the absence of any awareness of the movement involved.

But it is not only a question of the muscles being able to perform two different actions, the one voluntary and the other involuntary, and differing in the type of movement produced and in the part affected by the movement. It is possible to make a further statement concerning upper motor neuron paralysis for *a muscle may be paralyzed for a movement and yet be able to perform that same movement if the impulse of initiation originates below the cortical level.* The most striking example of this truth is that afforded by upper neuron paralysis affecting the arm and shoulder, and in which the patient, when asked to do so, is utterly unable to raise the affected arm from his side. Should such a patient awake in the morning and, without taking thought, commence to yawn, both arms, in going through the stretching movements that so commonly accompany yawning, will be raised from his side. The yawning-stretching movement is a reflex. Its object is to force stagnated venous blood out of the abdominal cavity and out of the veins of the limbs back into the heart again in order that it may be aerated. As such a reflex its initiation is sub-cortical. That a man who has his arm completely paralyzed by an upper motor neuron lesion may yet raise his arm when he yawns and stretches is a very remarkable thing: it is apt to be a complete surprise both to himself and to his attendants, but it should never persuade the clinician into suspecting that the paralysis is not genuine.

Since all these features of upper neuron paralysis go so strongly to confirm the dictum that the cortex and the cortico-spinal path are concerned only with definite movements and know nothing of the muscles that perform those movements, it is well to examine one or two curiosities of muscular movement and inquire if cortical knowledge of muscles is beyond human reach.

Since, as we have seen, an awareness of the part as an entity projected in space precedes a cortical ability to effect an alteration in position, it seems possible that the part of which we acquired awareness need not be a limb or any of the other gross subdivisions of the body. We can be well aware of the moulding of the surface of our bodies, and since much of this moulding is caused by the masses of muscle that lie beneath the skin, we may, at any rate, be said to be aware of some of our muscle contours. Is it possible that, knowing these contours, we could dictate an alteration of the contour by a cortical volition? Knowing the form of a certain subcutaneous elevation, and knowing it was made by muscle, could we make the muscle contract and so alter its surface form without having any desire to effect the alteration of the position of any part of our body represented by segments and joints? There is no doubt that by taking thought such things may be done. Even the small boy can do it. A small boy knows the elevation upon the front of his arm caused by the biceps muscle. It is his ambition to make that elevation prominent in order to show it to his rivals. A small boy can "show his biceps" as a cortically dictated act without the involvement of any cortical desire to flex his elbow or to rotate his forearm. The lump made by the biceps is cortically known to the small boy and its form may be cortically altered: and even if the cortex is unaware of the underlying muscle it is at least aware of its surface contour. Anyone who will try these things will find that such conspicuous masses as those made by the quadriceps extensor cruris, the glutei, or the muscles of the calf, may be readily moved in response to volition that goes no further than the simple command to alter the contour of the mass. These things may be carried much further. In gymnasts, in artists, models, and those who earn a livelihood by posing as classical figures upon the stage, an extraordinary cortical knowledge of the muscle masses may be developed. It is possible for a human brain by taking thought on these things to know of muscles as it knows of limbs and segments of limbs and to dictate alterations of the muscles just as it habitually dictates alterations in the positions of other realized and mobile parts. I have met a professional Adonis who could at will contract any superficial muscle as an individual entity. When we have seen such a one contract the serratus posticus inferior as an entity when asked to do so, we realize that the well-known dictum that movements not muscles are represented on the so-called motor area of the cortex needs some qualification. I can move my little finger to perfection; with practice and concentration an Oriental mummer may move a single segment of the rectus abdominis with an almost equal precision.

CHAPTER XXVII

THE UPPER MOTOR NEURON

Since there is peculiarity in the order of representation of awareness in the pallium—an order depending upon the method of acquirement—it is natural to expect that there will be a corresponding peculiarity in the order of the pallial representation of the initiatory mechanism for movement. From clinical evidence in man we know very well what regions of the pre-central area of the cortex govern definite bodily movements. Even if we abandon the hard and fast mosaic pictures of cortical areas laid down by the experimental pioneers of cortical localization, we must admit that there is something very definite in the order of representation of the pallial initiation of movement. When text-books of surgical anatomy lay it down as a sure guide in operations upon the brain that a bony ridge on the surface of the skull may be used as a landmark separating the arm and leg areas on the underlying cortex, we may be certain that there is a well-defined localization in the pallial areas that initiate voluntary movements in definite parts of the body. From below upwards in the pre-central cortex there are represented the centres for the motor control of the muzzle region, the face, the neck, the hand, the wrist, forearm, elbow, arm, shoulder, chest, trunk, hips, thighs, knees, legs, ankles, feet, toes and perineum. It is not a case of face, neck, shoulders, arms, forearms, hands and fingers: but the fingers are next the face in the order of pallial representation. Roughly we may say that, in the pallial area, the face is the lowest and the feet are the highest upon the lateral aspect of the cerebral hemispheres; but that the order of representation is not in simple anatomical sequence from face to feet, since the hand has intruded next the face.

Hughlings Jackson defined most of these areas so long ago as 1864 and, although in the interval our ideas as to cortical localization have grown less rigid, we may still accept the topographical depiction of the excitable motor areas in very much the same manner in which Hughlings Jackson established them.

Now the cells of the pallial motor area are of a peculiar kind, and those that are typical of this area in man are known as the *giant cells of Betz*. They are of a peculiar type because they *are* the specialized pallial cells for the initiation of so-called voluntary movements and they, or some of them, are giant cells because they have to be large cell bodies in order to sustain and to nourish the extremely long protoplasmic processes or neuraxons which pass from them through the brain and to the spinal cord as the cortico-spinal motor pathways.

When the neuraxons of the Betz cells of the pre-central motor area stream inwards from the surface to the centre of the brain they constitute a white fibre mass disposed at first in the manner of the disposition of their parent cells. The fibre tract streams inwards with the neuraxons of the cells governing movements of the foot above and the neuraxons of the cells governing movements of the face below. But as this leash of neuraxons proceeds downwards in the brain stem it undergoes an alteration in its disposition: it becomes twisted. As it passes between the great subcortical ganglionic masses to make its passage to the brain stem it arranges itself so that, although immediately beneath the cortex the fibres were arranged like the rays of a fan spread up and down along the line of the pre-central gyrus, a change is produced whereby the fibres from the bottom of the pre-central gyrus pass to the front and the fibres from the top pass to the back (see Figure 53).

The stream of neuraxons is elongated from above downwards as it passes through the *corona radiata* of the hemisphere: it is elongated from before backwards as it passes into the brain stem. In the rearrangement due to this twist, the highest fibres pass to the back and the lowest fibres pass to the front. This means that as the cortico-spinal tract passes between the basal nuclear masses, where it forms what is termed the *internal capsule* (see

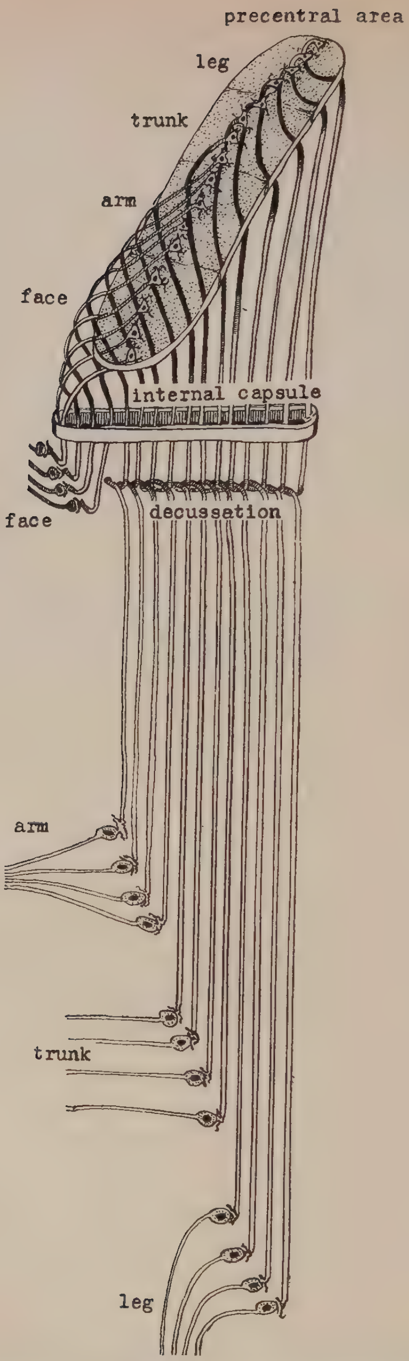

precentral area
leg
trunk
arm
face
internal capsule
face
decussation
arm
trunk
leg

Figure 53.—Purely diagrammatic plan of the arrangement of the fibres in the cortico-spinal motor pathway.

Figure 54), the neuraxons from the Betz cells initiating movements of the lips and muzzle region are in the front of the tract and the neuraxons of the Betz cells initiating movements of the toes are at the back. Moreover there has been a readjustment of the fibres from the Betz cells of the arm area, for whereas the arm is reversed in anatomical position on the pallium it has regained its anatomical sequence in the internal capsule. In the cortex the cells of the hand are next the face: in the capsule the fibres of the shoulder are nearest the head. There is, there-

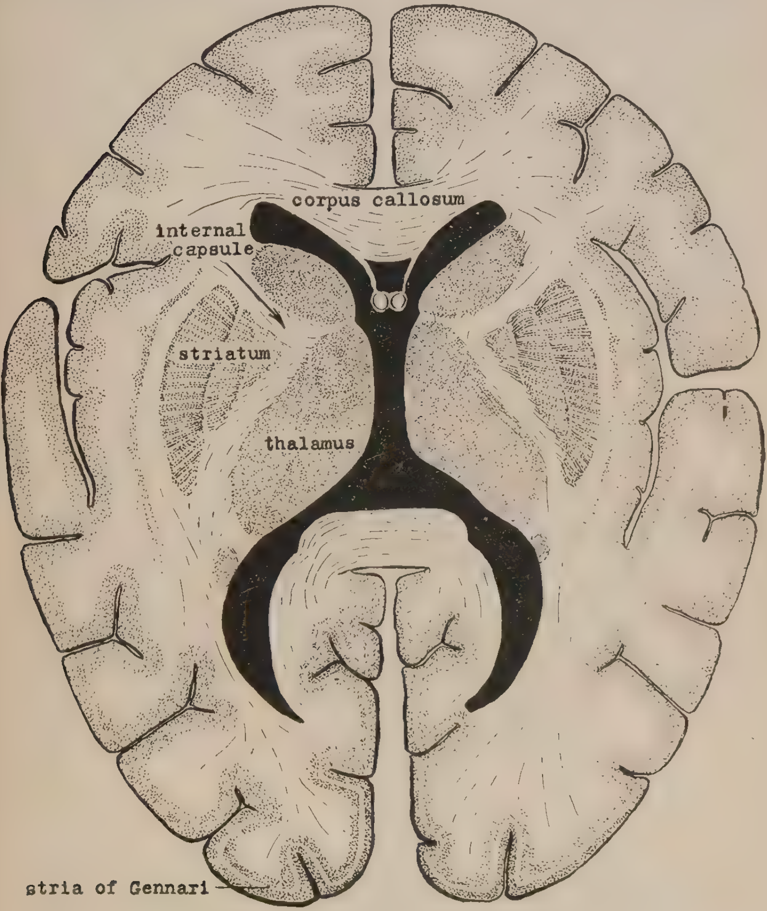


Figure 54.—Horizontal section through the human brain. The ventricular cavities are indicated in black.

fore, a stream of motor neuraxons passing from the white centrum of the cerebrum to the brain stem, to the medulla and to the spinal cord and in this stream there is always a definite plan of arrangement; the fibres are all sorted, and those dealing with the front end of the body are in front and those dealing with the back end of the body are behind. As we trace this bundle of neuraxons downwards through the internal capsule, through the crus cerebri, through the pons and medulla and into the spinal cord, we shall find that the neuraxons passing from the Betz cells come to an end by synapsing about new motor cells situated in the brain stem or in the spinal cord. The first to end in this way are those that are in the front of the fibre tract and that come from the Betz cells of the lowest part of the pre-central gyrus. These neuraxons come from cells situated in the area representing snout and face movements and they pass in the front of the internal capsule and through the crus and to the nucleus of the seventh or facial nerve, situated in the brain stem at the level of the hinder end of the pons. The last to end are those that are in the back of the fibre tract and that come from the Betz cells in the highest part of the pre-central gyrus. These are the neuraxons of the cells situated in the area representing the foot and they pass in the back of the internal capsule, through the crus, through the pons, through the medulla and right down the spinal cord to the anterior horn cells of the sacral region. Here they end in synapses around the anterior horn cells from which the great sciatic nerve is begot.

Now in this arrangement two things are quite clear. First it is obvious that from the cortical Betz cell there streams a main descending neuraxon which comes to an end somewhere at a lower level by entering into that network, known as a synapse, which brings it into relation with some other motor cell. This new cell may be high in the brain stem or in the lower end of the spinal cord. It matters not where the new cell may be; there is always a neurological entity consisting of a cortical cell and its neuraxon or *upper motor neuron* which comes to an end only when it meets a new cell which is the parent of the lower motor neuron.

The upper motor neuron, therefore, consists of a cortical Betz cell, situated in the pre-central region of the pallium, and its protoplasmic prolongation or neuraxon passing inwards in the white centrum of the cerebrum, through the internal capsule and the crus, to the motor nerve centres in the pons, medulla or spinal cord. We have seen that in the very formation of the central nervous system it is a fundamental principle that motor nerve cells are grouped towards the middle of the neural groove and, therefore, towards the anterior aspect of the brain stem and spinal cord. It is, therefore, obvious that the neuraxons of the upper motor neuron that are situated in the front of the tract will first meet the anterior motor cells and so give place to synapse and to the lower motor neuron.

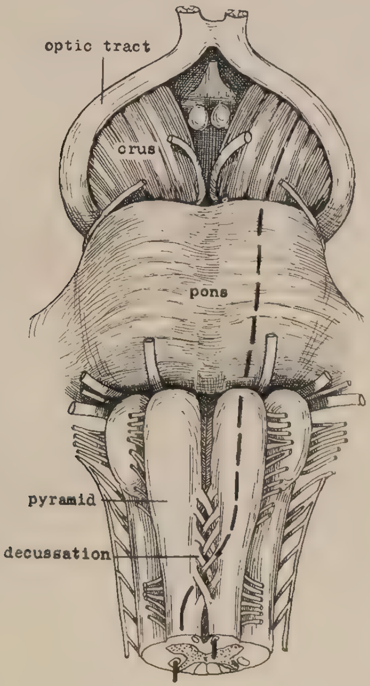


Figure 55.—Anterior (ventral) aspect of the brain stem to show the course of the cortico-spinal motor pathway.

Those neuraxons of the upper motor neuron that are at the back of the tract will go the farthest before they encounter anterior horn cells and so end in synapses. This is the meaning of the rearrangement and of the twist in the rope of the descending fibres from the cortical motor cells. As the tract descends, its fibres successively meet spinal anterior horn cells and so end. The fibres in front meet them first—the fibres at the back meet them last. The fibres from the face meet the nuclei at the level of the pons, the fibres from the area for the toes meet the anterior horn cells in the sacral region of the spinal cord. This produces a rather remarkable result, for the prolongations of the cells of the lowest part of the pre-central gyrus are the first to meet the motor cell of their lower motor neuron and the prolongations of the cells of the highest part of the pre-central gyrus are the last to meet their anterior horn cells of the lower motor neuron. The neuraxon of a cell of the area for the face will therefore run only for the few inches that separate the cell at the lower end of the cortical motor area from the nucleus of origin of the facial nerve, whilst the neuraxon of a cell of the area for the toes runs the distance of feet that separates the cell at the upper end of the cortical motor area from the anterior horn cell which begets the great sciatic nerve (see Figure 53). Now the longer the neuraxon which the parent nerve cell has to sustain and nourish, the larger must that parent nerve cell be. It, therefore, results that the Betz cells of the pre-central gyrus or motor pallial area are larger and more typically of the form of *giant pyramidal* cells at the top of the area and are smaller and less typical at the bottom.

This then is the fashioning of the great cortico-spinal or *pyramidal tract*. It consists of the neuraxons of the pyramidal cortical cells of the motor pallium; it runs as a band, flattened fore and aft and elongated in a vertical direction, into the substance of the brain as part of the corona radiata: the band becomes twisted so that it is flattened laterally and elongated fore and aft, with the fibres from the top of the band passed to the back and those from the bottom of the band to the front. As such a band it runs through the crus, the pons, the medulla and to the end of the spinal cord, ever diminishing as it goes by the ending of its fibres as synapses around new motor cells. But a curious thing happens to it on its passage from the medulla to the spinal cord, for the pyramidal tracts of the two sides of the medulla turn towards each other, their fibres interlace, and for the great part change across to the opposite side from that on which they originated. This interlacing and changing over is carried out on the anterior surface of the upper part of the spinal cord. The passage of the fibres from the one side to the other is a striking naked-eye feature and it is known as the *decussation of the pyramids* (see Figure 55). All the fibres however do not change sides here: the decussation is not total and some neuraxons continue upon their course down the same side of the spinal cord as that upon which they originated. It thus results that there are two cortical spinal tracts in the spinal cord below the level of the decussation of the pyramids; there is the *lateral or crossed pyramidal tract* and the *anterior or direct pyramidal tract*, upon each side of the spinal cord. But it must be remembered that although the anterior tract is direct in so far as it does not share in the great decussation of the pyramids it is not direct in the sense that it is a pathway from one cortical

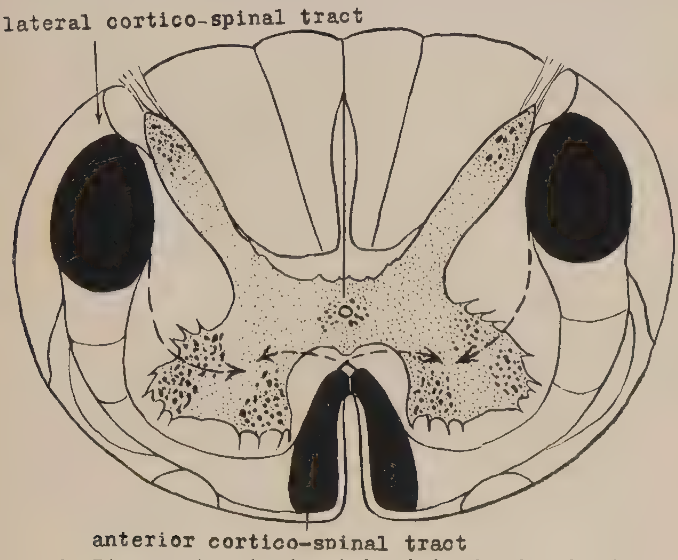


FIGURE 56.—Diagrammatic section through the spinal cord to show the spinal tracts. The cortico-spinal motor pathways are black.

motor area to the muscles of the same side of the body. The fibres of the anterior pyramidal tract all pass to anterior horn cells of the opposite side of the cord, but they do not effect this crossing in bulk; they pass away one at a time across the anterior commissure and so eventually make connection with an anterior horn cell which is the parent of a lower motor neuraxon of the opposite side of the body from that upon which they have origin (see Figure 56).

CHAPTER XXVIII

THE CORPUS STRIATUM AND ITS PRIVATE PATH

The descending fibres from the cortical motor area all cross to anterior horn cells of the opposite side from that on which they originate, so that the voluntary movements of one side of the body are evoked from the pallial area of the opposite side.

In the brain stem the neuraxons from the Betz cells of the area for the head pass directly across into the motor nuclei of the cranial motor nerves. Below this level the great crossing is done in the decussation of the pyramids, and still further down the fibres of the direct or anterior pyramidal tract pass across at intervals in the anterior commissure of the cord. The fate of all the neuraxons of the Betz cells is the same; they cross to the opposite side of the body and end in a synapse about a new motor cell from which the neuraxon of the lower motor neuron takes its origin. In this respect we have repeated the story of the sensory tracts in the spinal cord, and the likeness may be carried further. We have seen in the case of the sensory tracts in the cord that, so far as sensation is concerned, they form a series of private paths. In exactly the same way with movement, the cortico-spinal or pyramidal tracts, descending from the pallial motor area, constitute only one of the private paths of the upper motor neuron segment. In man, the cortico-spinal private path has become of such dominant importance that the other private paths are of comparatively minor significance, but this is merely a human specialization. In the reptiles there is no cortico-spinal tract and therefore the pallium cannot exert its influence upon the lower motor neuron and so upon movement. In the lowest mammals the cortico-spinal tract extends only into the brain stem and so enables the pallium to exert a motor influence upon the nuclei of origin of the cranial nerves. In certain marsupials the cortico-spinal tract extends so that its neuraxons come into relation with the anterior horn cells of the brachial nerves and so the pallium may exert its influence on fore-limb movements. In all mammals lower than the Primates the cortico-spinal tract extends only for varying distances down the spinal cord.

It is only in the Primates that it runs its entire length and only in man that it reaches its full development and becomes the dominant private pathway of movement. Since the stage of development of the cortico-spinal path is an index to the degree which initiation of movement finds lodgment in the cortex, it is reasonable to inquire into the extent and the importance of the motor cortex in different animals. Here there is a vast amount of experimental work available. The anatomical position and the extent of the excitable motor cortex are known in a wide range of animals; the results of the experimental removal of the motor area have been recorded by a number of observers in an almost equally wide range of forms. The anatomical and the experimental findings are in harmony with the knowledge gained from a study of the cortico-spinal tracts. We may say that in an ascending animal scale, the whole of the excitable cortex may be removed without causing any impairment of movement; that its removal may cause a temporary impairment in movements of the snout region and fore-limb; that it may cause a temporary paralysis of the snout region and fore-limb, a temporary paralysis of the whole of the opposite side of the body, or—in man—a permanent paralysis for all "voluntary" movements of the whole of the opposite side of the body. It is to be noted that in all cases, even in man, the face and fore-limb are most profoundly affected and that recovery, if it takes place, is much more rapid and more complete in the leg than in the arm. Obviously in all this there is demonstrated a growing importance of the pallial area and of the cortico-spinal pathway. Starting as, apparently, a mere adjunct to the mechanism of movement, the cortex seems to have usurped the initiatory function for all those movements which we have defined as the alteration of the position in space of a part the spatial relations of which are cortically realized. Moreover this usurpation has obviously taken place in the order in which the awareness of parts of the body was gained. In us the complete awareness of our bodies, the complete dominance by the pallium of movements of the type we have defined, and the full development of the cortico-spinal tracts are all expressions of the same great fact.

But it is apparent that there is some older motor initiatory mechanism from which the pallium has, in us, usurped certain of the more important functions. In those mammals in which the whole motor cortex may be excised without ultimate impairment of movement, there must be some co-ordinating and initiating centre responsible for complex bodily movements: there must in fact be some centre for initiating those co-ordinated movements that are in character intermediate between the simple reflexes carried out in the spinal cord and the deliberate movements initiated in the human pallium. Apart altogether from the very clear evidence to be derived from the study of inter-cerebral pathways and from the phylogenetic story of the brain itself, there are direct experimental findings that point clearly to the fact that the complex basal ganglionic mass known as the *corpus striatum* (see Figures 49 and 54) is the great cell station for the initiation of all those movements that, in lower vertebrates, may be said to be instinctive or innate as distinct from mere reflexes on the one hand and from the considered or deliberative type of human acts on the other. A dog may have the whole of its excitable motor cortex removed, and if the operation be done on a young animal and other parts of the brain are not damaged in the performance of the operation, the animal may still carry out all the movements appropriate to an ordinary dog. A dog deprived of its motor cortex not only rehearses all the movements that are essential to its life preservation and to the continuance of its own existence and the existence of its race, but it also carries out all the play actions peculiar to normal puppies and does the many unessential acts that are characteristic of the ordinary dog. But if the corpus striatum is included in the removal, the dog has to be kept alive by artificial means, for even the instinctive movements requisite for the obtaining of food, the avoidance of danger and the adjustment of its body in space are lost after the operation. Such a dog is thrown back upon the simple reflexes derived from the inter-action of the dendrons of its lower sensory neuraxons upon the anterior horn cells of its lower motor neuraxons in the spinal cord. The whole complex history and the complicated anatomy of the corpus striatum need not be discussed; it is enough to realize that from anatomical, embryological and experimental evidence we are justified in regarding the striatum as the great cranial ganglionic centre for the initiation of all those complex movements which we may class as instinctive or innate, but which have as their distinctive character that their initiation does not depend upon a previous awakening of cortical awareness. In harmony with this finding is the fact (established by Rogers, 1924) that the corpus striatum of the marsupials is electrically excitable, whereas in the higher mammals the motor area of the cortex will alone produce movement when stimulated by electrodes. Even by this crude test there is shown a translation of function from the striatum to the cortex. Since the striatum is the great primitive and essential initiatory centre for all the routine movements of the typical mammals, we may justly ask what is the rôle played by the striatum in initiating movements in man. We have seen that there is a steady sequence in usurpation of function; the pallium is dominating the striatum and taking from it the right of initiating movement of a very definite kind. We have defined the type of movement initiated by the pallium: we realize the nature of movement initiated by the striatum: it is the case of the considered, deliberative movement of a part of which we have cortical awareness, on the one hand, and the movement which is instinctive or innate and in which there is no awareness or realization, on the other. So far as man is concerned, we may say that the pallium has taken over the initiation of all movements which are the outcome of cortical awareness of parts of the body. Surely it gives us a great insight into human motor activities when we realize that it is justifiable to say of the corpus striatum in man that "its true motor function has gone, never to return" (Kinnier Wilson, 1914). Human movement is on a plane altogether different from that of the typical lower mammals. In man all movement of the skeletal parts of the body are cortical, considered, deliberative actions if they are raised at all from the level of pure reflexes.

But though in man the corpus striatum has for ever ceased to be an initiator of movement it still exerts its influence upon the whole complex of which human movement is compounded. This influence consists essentially in a steadying of the movement and a control of the tone of the muscles carrying out the movement. The striate influence is carried to the anterior horn cell and the lower motor neuron by a complicated fibre tract known as the *lenticulo-rubro-spinal tract* (see Figure 57).

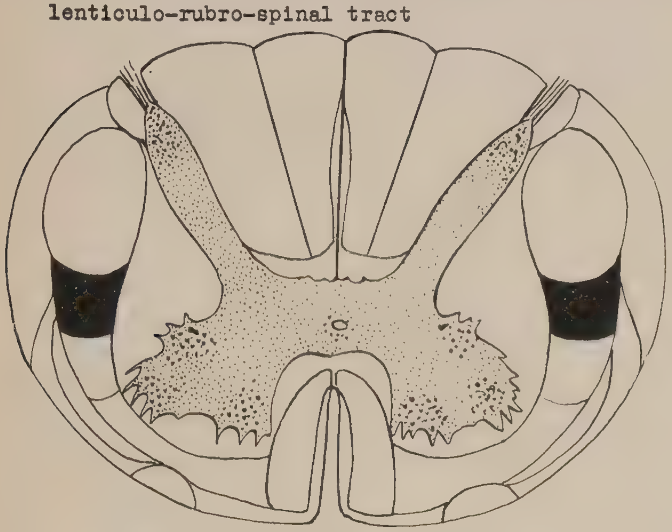


FIGURE 57.—Diagrammatic section through the spinal cord to show the spinal tracts. The lenticulo-rubro-spinal tract is black.

This, the second private path of the upper motor neuron, runs in the lateral columns of the spinal cord in close proximity to the crossed pyramidal or lateral cortico-spinal tract. Interference with this private path or abeyance of the normal functions of the corpus striatum does not produce paralysis, but it leads to a variability of muscle tone, a tremor in the performance of movement, and at times to the production of involuntary movements. Such interference with striate influences is seen in what is termed the Parkinson syndrome in which is included such affections as *paralysis agitans*; and in certain peculiar forms of chorea-athetosis. In dealing with sensation we have noted the presence of a highest sensory neuron, a connection between the thalamus and the cortical field of awareness of the body. In the case of movement the arrangement is not so clear, since the pallium seems to have so wholly usurped the functions of the corpus striatum. What the cortico-striate connections are in man cannot be dogmatically stated, but it would certainly seem to be a case of functional connection even if the anatomical bond is not clear. In man the pallium has so dominated the striatum as the initiator of movement that it seems to be singularly aloof from the striatum in its anatomical connections. Nevertheless, the striatum still has its own powers and, as Kinnier Wilson has observed, "The normal corticospinal system is unable to prevent the effects of striatal disease from making their appearance."

The typical vertebrate mechanism for the initiation of innate or instinctive movement may have been supplanted in man—but it still has its revenges.

CHAPTER XXIX

THE LABYRINTH AND ITS PRIVATE PATH

That an animal should be able to move is not enough. Movement may consist either in the alteration of the position of a movable part, or in the translation of the animal as a whole in space: whichever it is, it is not performed as a single isolated act; it must be carried out in relation to other factors. Movement of an individual part must be carried out in relation to the body of the animal itself: movement can only be one element in a harmonious disposition of the parts in a definite posture. We cannot raise one foot from the ground as an isolated act, for thereby we disturb a pre-existing posture, and simultaneously with the raising of the foot there must be a readjustment of our whole body poise. If we wish the movement to effect our translation through space we cannot undertake it as an isolated act, for it must necessarily have relation to the supporting surface that bears our weight and to the force of gravity acting on our bodies. There must necessarily be numerous adjusting mechanisms by which isolated muscular actions are fitted in with the complexities of posture and so are carried on with regard to all the other factors that determine the relation of our parts to our own bodies and to the environment in which we move.

We have seen that all the instreaming afferent fibres that run to the central nervous system do not evoke sensation; they do not enter into consciousness and become translated into a named feeling. There is a great group of silent impulses for ever streaming in to the central nervous system; impulses that are of the utmost importance in producing a self-adjusting mechanism, but which do not make themselves felt, since their office is an automatic one with which the higher centres have no concern. This silent system of instreaming impulses is known as the *proprioceptive system.*

We may say in general that in performing every movement that involves orientation of the head and body of a higher mammal there must be adjustment by which it can be carried out in relation to the other parts of the body, to the sustaining surface, and to gravity. In addition to this there is, in the members of our phylum, and preeminently in us, another factor, for normally movement must be carried out in relation to the distant environment. Now impulses from the other parts of the body, and from the organs which inform our central nervous system of orientation with regard to gravity, may perhaps rightly be termed proprioceptive; but the distant environment is learned of by different channels and different sense organs and to these the term proprioceptive cannot be applied. It is part of a very definitely human trend of development that our optical orientation reflexes, which are truly *exteroceptive*, are becoming of increasing importance and this at the expense of one of the earliest vertebrate orientating mechanisms—the primitive *otolithic organ*. This, the first and most important of the self-adjusting mechanisms, consists of a little sac containing fluid in which a solid otolith is free to move and excite the sensory cells lining the sac by its movement. This primitive static regulator was developed in close anatomical association with the organ of hearing. In lower vertebrates it may manifest itself as lateral-line organs and otocysts; but in order to embrace all the varied types of this organ we will be content to term it the *labyrinthine system*. In brief, such a system consists of a series of tubes and chambers containing fluid—somewhat on the lines of a spirit-level. But instead of a bubble giving a visual appreciation of the movements of the fluid, the moving fluid and the otoliths suspended in it react on the sensory hair cells projecting into the tubes. As the hairs sway in the moving fluid silent impulses stream inwards along the vestibular nerve. The animal moves its head, the fluid in the tubes and chambers of the labyrinthine system is stirred in a definite direction, the hair cells are bent by the moving fluid and silent impulses of orientation pass inwards to the central nervous system. In us this system is represented by the three *semicircular canals* and their adjuncts the *saccule* and *utricle* (see Figure 58): and in us the semicircular canals are so arranged that the fluid movements within them can inform of all directions in space. We may nod our heads backwards and forwards as when we signify "yes," we may nod from side to side, or we may rotate, as in the pantomime method of saying "no." In each of these movements, and in all variants of them, we create a fluid movement in the labyrinthine system and the sensitive prolongations of the cells which sway to and fro in the moving fluid may send silent messages to the central nervous system. These impulses pass by way of Scarpa's ganglion and the vestibular nerve to certain nerve cell stations in the medulla. The immediate cell stations of the labyrinthine system are known as the lateral vestibular nucleus (nucleus of Deiters), superior vestibular nucleus (nucleus of Bechterew), the medial vestibular nucleus and the descending vestibular nucleus. These nuclei all lie close together in the brain stem beneath the cerebellum. Anatomically the cerebellum rises from the brain stem in the neighbourhood of the centres for the labyrinthine impulses: phylogenetically it is begot in relation to the instreaming silent proprioceptive stimuli.

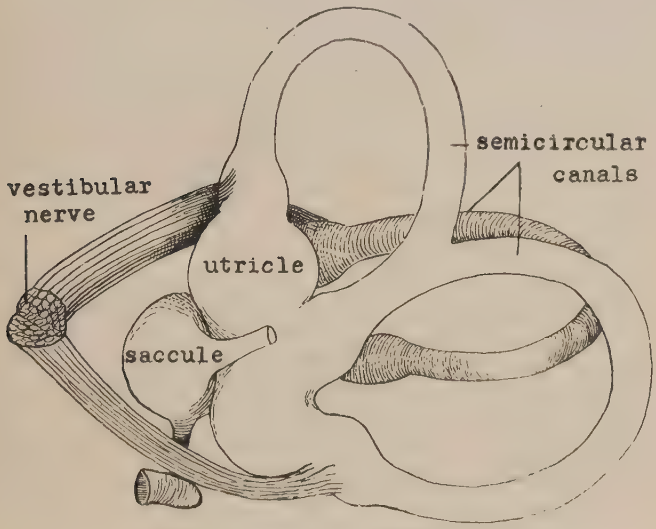


FIGURE 58.—The human labyrinthine system.

But the labyrinthine system, though it be the parent of the cerebellum, is not limited to the cerebellum for its central connections: nor does the cerebellum usurp the functions of the labyrinthine system: it has its own well-defined rôle to play in the complex of movement. Apart from the cerebellum, the vestibular nuclei have other connections which are of the utmost importance. First, from the vestibular nuclei, tracts lead into the *posterior longitudinal bundle* or fasciculus longitudinalis medialis and, thereby, connection is made with all those nuclei which give out impulses for the movements of the eyes (see Figure 16). It is by the posterior longitudinal bundle that the vestibular system makes connection with the primitive *photostatic* or light-guiding system (dealt with in Chapter XL); the silent impulses streaming in from the semicircular canals are correlated with the impulses arising from the photostatic organs. By way of the posterior longitudinal bundle and its connections the light-guiding sense and the gravity-orientating sense are brought into harmony and the silent stimuli of poise are knitted into a neurological entity. Later in phylogenetic development, when the light-guiding sense is developed into a true visual sense, the postural impressions, deduced from the actual picture of our surroundings, are correlated with the stimuli of poise derived from the movements of the fluid of our spirit-levels. It is at this stage that visual sensations are like to usurp some of the functions of the older mechanism. We depend so largely upon what we learn by the eyes that we may overlook the silent impulses of the labyrinth. We take our bearings by distant objects and we know of our orientation in space, since we are familiar with other orientated objects. Our eyes may even persuade us to mistrust our labyrinths; when our labyrinths would tell us we are at rest we may yet believe we are in motion when we see the other train move out of the station. It is because these visual stimuli are cortical that they are so much considered and, being among the aristocracy of high-level impulses, they are dominating the impressions correlated at a lower level. How completely we have come to depend upon our eyes to the neglect of our spirit-levels has been learned by the aviator, for it is a common experience that, on emerging from a bank of cloud in which visual orientation has been impossible, the flying man finds he has become completely disorientated with regard to the earth.

It is by route of the posterior longitudinal bundle that labyrinthine impulses may influence ocular movements and produce, in cases of labyrinthine disturbance, those curious rhythmical side-to-side movements of the eye-ball known as labyrinthine nystagmus.

Although the impulses from the labyrinth may properly be classed among the silent group, nevertheless they may force their way to higher levels and so to consciousness.

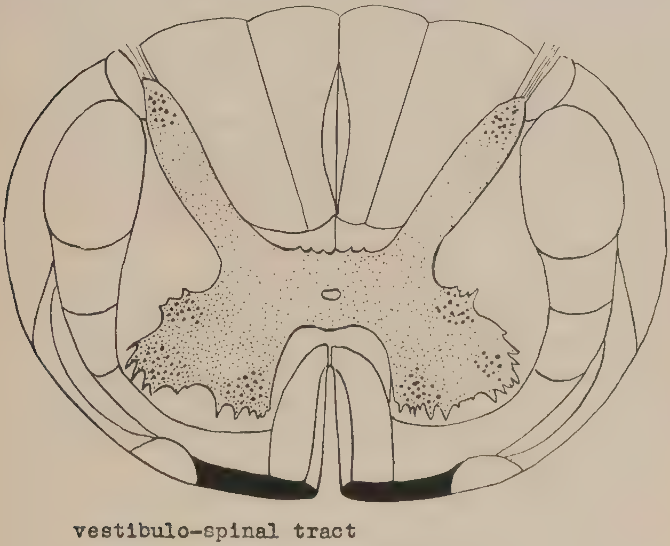


FIGURE 59.—Diagrammatic section through the spinal cord to show the spinal tracts. The vestibulo-spinal tract is black.

Unusual and violent agitation of the hair cells of the spirit-level system may demand recognition at higher levels and be registered as the subjective feeling of vertigo. Such feelings of vertigo cannot be produced in those in whom the labyrinth is lacking even though they be violently rotated; and labyrinthless deaf-mutes will drown if they are submerged under water, since without visual impressions they have no sense of orientation. It is useless to struggle under water if you cannot tell if you are going up or down.

Even more important than the cranial connections of the vestibular nerve are its connections in the mid brain and its private pathway to the spinal cord. The work of Rademaker has shown very clearly that the great centre for the discharging of the labyrinthine influences is that conspicuous nucleus, which lies in the brain stem at the level of the emergence of the third cranial nerves, and is known as the *red nucleus* (see Figure 49).

It is from the vestibular nuclei and the red nucleus that the *vestibulo-rubro-spinal tract* descends in the spinal cord.

This, the third private path of the upper motor neuron, runs downward in the anterior column of the cord, in the immediate neighbourhood of the anterior cortico-spinal tract (see Figure 59). By this tract the labyrinthine system exerts its influence on the common path of the lower motor neuron, and so on the mechanism of muscular movement. The influence is such that it permits righting movements to occur when disorientation has made them necessary and it regulates the balancing of the moving parts of the body so that it produces a harmony of balance during the performance of a movement. If the private path of the labyrinthine system to the anterior horn cell be interrupted there is a loss of co-ordination of movement and this loss displays itself in a characteristic staggering or unbalanced stumbling of the moving part. This peculiar derangement of movement is best termed *titubation*: it is the stumbling of a moving part cast off from the influence of the spirit-levels.

We have seen that the cortex has very thoroughly usurped the functions of the corpus striatum and the striatum can only obtain its revenges by way of its private path. Evidently the same story is unfolding in the case of the labyrinth. The cortex by virtue of its awareness has dominated the initiation of all the best of movement: by virtue of its visual guidance it is usurping the functions of the labyrinth. We are passing, even in orientation, from self-regulation to cortically considered control.

CHAPTER XXX

MUSCLES AND MOVEMENT

Since it is movements and not muscles with which the cortex deals, it follows that when a cortical volition for movement is inititated an extremely complicated mechanism is involved, for, with the very rarest exceptions, muscles taking part in voluntary actions do not act as individual entities but as groups.

A great complexity of acting muscles is involved in carrying out even the simplest of movements. In order to understand the relation of muscles to movements we must try to eliminate from our minds all that teaching with which the text-books of human anatomy are replete and which deals with what are termed the actions of muscles. The action of a muscle as it is conceived in such books is the mechanical result of its individual contraction: either the effect produced by pulling on the isolated muscle in the cadaver, of substituting a mechanical contrivance with its attachments, or by electrically stimulating the individual muscle in the living subject. If we remember the general truth that muscles practically never act alone as individuals, and that nearly all muscles may act in four separate capacities, it is easy to see how little utility there is in the common teaching with regard to the action of muscles. If I refer to a standard work on human anatomy in order to ascertain the action of the flexor carpi ulnaris I find the matter dismissed with the statement that "the flexor carpi ulnaris flexes the wrist and slightly adducts the hand."

But in the living subject there are seven different combinations in which the action of the flexor carpi ulnaris is essential to the proper performance of the simplest voluntary movements.

In order to understand the nerve regulation of muscular movement it is necessary first of all to define the ways in which muscles may act and make some slight study of the common laws governing these actions. For the most part muscles act in groups; many muscles are involved in producing an apparently simple action, and all the members of the group involved do not act in the same capacity. There are four main rôles in which a muscle may be employed, for in producing a movement it is necessary, in the majority of cases, to call upon different muscles to act in the capacities of (1) agonists or prime movers, (2) antagonists, (3) synergics and (4) fixators.

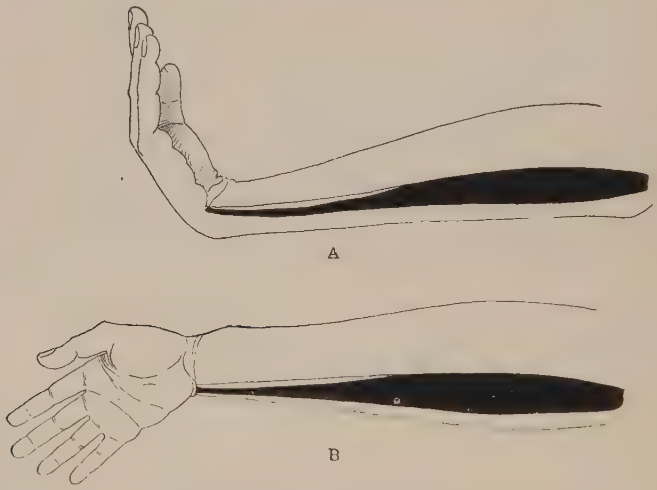


Figure 60.—The actions of the flexor carpi ulnaris as an agonist. A, volition to flex the wrist; action with the flexor carpi radialis; B, volition to move the hand to the ulnar side; action with the extensor carpi ulnaris.

A muscle is employed as an *Agonist or Prime mover* when its action directly produces the alteration in position of the part which is dictated by the cortex. When I wish to bend my finger, the flexor muscles of the finger act as agonists. There are certain definite laws governing the action of all agonists. As a general rule it may be said that an individual muscle does not act alone as an agonist. In cases of minimal movement and in the movement of certain parts, such as the upper eyelid, a single muscle may do all that is necessary; but in the majority of movements in which any force is involved, or any considerable part of the body is moved, the work is undertaken by a group of agonists all having the power to produce the desired alteration of position. It is a curious fact that a muscle acting in a living body as the result of a volition does not necessarily produce the same action as is effected by pulling upon the isolated muscle in the cadaver or as is produced by a mechanical contrivance inserted between its skeletal points of attachment. When traction is exerted on the sterno-mastoid muscles isolated in the dead body, it is easy to see that they tilt the head backwards, since the mastoid processes and superior curved line of the occipital bone to which they are inserted are situated behind the hinge of the occipital condyles upon which the skull pivots. I have only to turn to a text-book on human anatomy to find their action described thus: "both muscles acting together extend the head." Nevertheless in the living subject both sterno-mastoids acting together inevitably flex the head, for they tilt the head forward, and not backward when they contract in response to a volition. Another common error in the teaching of the action of muscles is to ascribe to the muscle all the actions that the complex anatomical arrangement of its fibres will permit in the dead body. By pulling upon isolated portions of many of the large sheet-like muscles a variety of movements may be produced. But in the living body it is the rule that such a muscle produces only one definite action as an agonist, and the rest of the actions of which it is anatomically capable are evoked only when it acts in some capacity other than that of an agonist. This is especially the case when by an anatomical arrangement of its fibres a muscle is capable of producing opposed movements of a part in the cadaver. Acting as an agonist the muscle in the living subject will produce one movement, and the other will be evoked when it is acting in another capacity. It is a very important thing to remember that no muscle will act as an agonist in producing a desired movement if gravity itself will produce the movement for it. This simple fact is often overlooked in the examination of living subjects and, as we shall see, in discussing the action of antagonists, it is capable of producing some very deceptive conditions of muscular action. Two other factors govern the action of agonists, as they do of all muscles. It is a peculiarity of muscle that it always acts to its utmost. For a minimal action therefore it is not necessary for large muscle masses to be involved, for each fibre acts to the limit of its power and only sufficient fibres are called into action to perform the desired task. As the task becomes more arduous more fibres are brought into action, and every fibre which acts does so to its full capacity. A muscle does not necessarily act as a whole, nor are all muscles capable of performing the action necessarily involved: but muscle after muscle is called upon to assist the one which is initially elected as the agonist, and in this matter there is a definite regulation of order in calling for assistance.

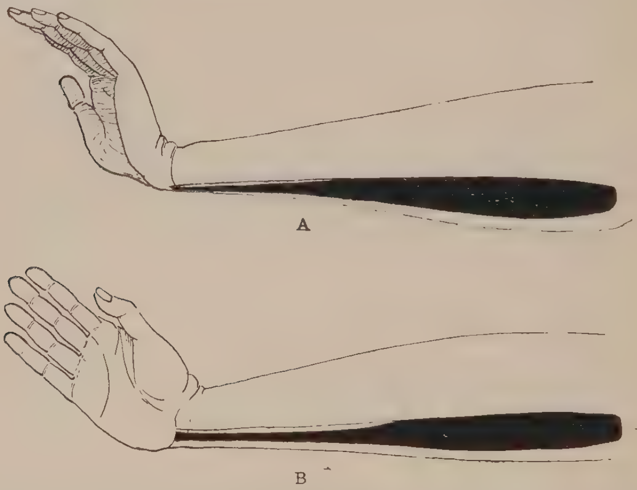


FIGURE 61.—The actions of the flexor carpi ulnaris as an antagonist. A, volition to extend the wrist; action with the flexor carpi radialis. B, volition to move the hand to the radial side; action with the extensor carpi ulnaris.

The second capacity in which muscles act is as *Antagonists*. Antagonists are the muscles that produce the action opposed to that initiated by the cortex and carried out by the agonists. If we wish to bend a finger the flexors of the finger are the agonists, the extensors of the finger are the antagonists. Practically every muscle in the body has its antagonist, and it is obvious that when the agonist is called into action by the cortex a change of some sort must be produced in the antagonist. In its simplest form we may say that when an agonist contracts and produces a movement the antagonist must relax in order to allow the part to be moved. We may say that the impulse which activates the agonist *inhibits* the antagonist: but to dismiss the rôle of antagonists merely as being that of suffering inhibition is to overlook the great functional importance of their action. In most ordinary muscular actions the relaxation of the antagonists is certainly not a mere passive process of inhibition of activity: for the antagonists are the essential controllers and governors of the action of the agonists. When agonists produce the desired movements the antagonists pay out the slack, as a man pays out a rope of which a turn is made round a windlass, and only sufficient slack is paid out, in a guarded and graduated fashion, to ensure steadiness and precision in the action. The more precise the movement required of the agonist the more exacting the rôle of the antagonist, and in movements which are themselves of very small range, but are performed with great nicety, a great deal more muscular energy is involved than the mere mechanical performance of the movement warrants. When resistance to the action of the agonist comes from without, as in all opposed movements, the part played by the antagonists becomes superfluous, and in these circumstances their rôle is merely that of passive elongation: their action is truly inhibited. We have already seen that in unopposed actions in which gravity will perform the movement of volition the agonists cease to act. Under these conditions there is produced that curious phenomenon that has led to so much clinical misunderstanding and that is known as the *Action of Paradox*. If we wish to bend the trunk backwards, the action is initiated by contracting the muscles of the back and these, pulling on the spinal column and the skull, are the agonists producing the desired movement. But directly the skull and upper part of the trunk are sufficiently moved from the vertical for gravity to complete the act, the agonists cease to contract, and their antagonists, the muscles of the front of the body, come into action. During the process of tilting the body backwards it is the muscles of the abdominal wall that come into play, not because they are the muscles that produce the movement

—that is done by gravity—but because they are the muscles which prevent gravity taking charge and so toppling the body over.

Equally important is the third rôle in which muscles are employed in producing and regulating movements. This third rôle is that of acting as *Synergics*. Many muscles in their course from origin to insertion pass over more than one joint, and thus anatomical arrangement permits them to exert their influence upon more than one moving part. It may therefore happen that a muscle can do more actions as an agonist than are required by the volition. When the volition directs the performance of a certain definite movement, and the muscles which perform this movement are also capable of producing other movements not included in the volition, then other muscles will be called upon to counteract the production of these undesired movements. The muscles which bend the fingers will also bend the wrist. If we wish that the fingers alone shall be bent, it is necessary that muscles which extend the wrist shall be brought into play to counteract the flexion that would otherwise be produced. If we wish to grasp with the fingers, the wrist is first held firm by the wrist extensors, and if still more force is brought into the action, the wrist

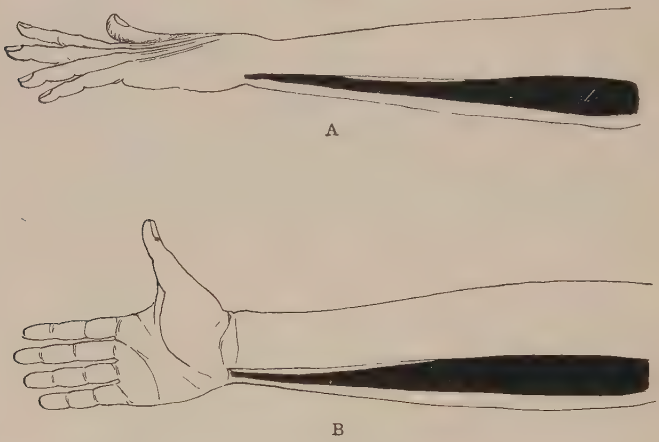


Figure 62.—The actions of the flexor carpi ulnaris as a synergic. A, volition to extend the fingers; action with the flexor carpi radialis. B, volition to move the thumb towards the radial side; action with the extensor carpi ulnaris.

extensors actually pull the hand back so that the finger flexors may exert more power. Were it not for the synergic action of the wrist extensors the wrist would bend with the fingers and all power to grasp would be lost. The action of synergic muscles is of prime importance in the regulation of movement and the loss of synergic function produces serious disassociations of movement which will be examined later. The last separate function of muscles in the production of regulated voluntary movements is that of acting as *Fixators*. If we wish to perform some act of precision with an instrument held in the fingers, the agonists which produce the movement are called into play; the antagonists exert their regulating control to the utmost; the synergics prevent undesired actions of the agonists. But, as the business becomes more exacting, fixation becomes necessary: fixation of the wrist, of the elbow, of the shoulder; and when all our attention is concentrated upon some very delicate manipulation, which may require only one tiny muscle for its performance, we may in fact have to employ a wide series of muscles in order to secure that immobility and fixation of parts necessary for securing the utmost precision.

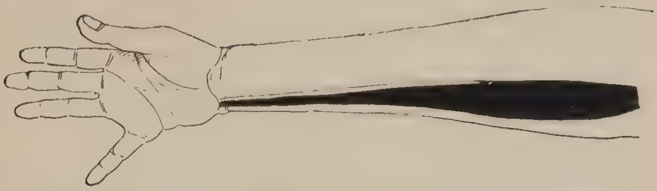


FIGURE 63.—The action of the flexor carpi ulnaris as a fixator. Volition to move the little finger to the ulnar side; acts as fixator of the pisiform bone.

We may now return to the text-book statement that the action of the flexor carpi ulnaris is that it "flexes the wrist and slightly adducts the hand" and attempt to ascertain what actions of this very simple and not vastly important muscle can easily be detected by palpation of the tendon in our own wrists.

(1) If we wish to flex the wrist the flexor carpi ulnaris acts with the flexor carpi radialis as an agonist (see Figure 60).

(2) If we wish to move the whole hand to the ulnar side the flexor carpi ulnaris acts with the extensor carpi ulnaris as an agonist (see Figure 60).

(3) If we wish to extend the wrist the flexor carpi ulnaris acts with the flexor carpi radialis as an antagonist to the wrist extensors (see Figure 61).

(4) If we wish to move the whole hand to the radial side the flexor carpi ulnaris acts with the extensor carpi ulnaris as an antagonist to the extensor ossis metacarpi pollicis (see Figure 61).

(5) If we wish to extend the fingers the flexor carpi ulnaris acts with the flexor carpi radialis as a synergic to the extensor communis digitorum and the extensor longus pollicis (see Figure 62).

(6) If we wish to move the thumb from the fingers in a radial direction the flexor carpi ulnaris acts with the extensor carpi ulnaris as a synergic to the extensor ossis metacarpi pollicis (see Figure 62).

(7) If we wish to move the little finger from the other fingers in an ulnar direction the flexor carpi ulnaris acts alone as a fixator of the pisiform bone for the action of the abductor minimi digiti (see Figure 63).

Obviously the part played even by the flexor carpi ulnaris in common movements is a very complicated one. It is far more complicated than we would imagine by reference to its described action in the anatomy books. It may be well that the motor cortex does not concern itself with the details of muscles, and is content to do no more than order movements. But it is equally obvious that there must be some controlling mechanism that looks after the proper co-ordination of agonist, antagonist, synergic and fixator else these factors in the production of movement might become dissociated.

CHAPTER XXXI

WHAT THE CORTEX CANNOT DO

The alteration of the position in space of a part the spatial relations of which we realize—in other words, a cortically initiated movement—is an extremely complex affair. Numerous muscles take part in the action, and the part that each one plays is a well-established and a preordained one. We have seen that a muscle may act as an agonist, antagonist, synergic or fixator and the rôle that it takes in the combined action that represents a cortically initiated movement is a predetermined one. In every movement a particular muscle plays its proper rôle, it may be as synergic or as agonist or in some other capacity, and this rôle is definitely assigned to it in that movement. We cannot, by thought, cause it to alter its rôle, for the arrangement of the details of a movement is carried out by something over which we have no control. Not only are we unable to cause any alteration in the sequence of the muscular activities combined in the carrying out of any movement, but we are precluded from prohibiting any of the concomitants of a cortically initiated action. We cannot alter the sequence in which muscles are called on in performing an act; we cannot change the rôle that each individual muscle plays; nor can we voluntarily dispense with a contributory muscular action, even though such action may appear quite unnecessary in the performance of the act of volition. As I sit at ease in a chair with my elbows resting upon the arms, the muscles of the abdomen and loin, which pass from the pelvic girdle to the ribs, remain in a state of rest and are soft and flaccid when palpated. If, however, I press one elbow downwards upon the arm of the chair it will be noticed that, though the movement may have been very slight and the force employed have been minimal, the muscles of the abdomen and loin of the same side at once undergo a contraction. The muscles that pull my arm downwards in this minimal action are the pectorales and these muscles take origin from the ribs. In certain, and forcible, actions of the pectorales their contraction tends not only to pull the arm down to the ribs, but it may also exert its force on the ribs and so tend to pull them up towards the arms. This is the case when the arms are employed in tree climbing, for the animal having grasped a branch and so stabilized the fore-limbs contracts the pectoral muscles and hauls the body upwards to the arms. In this action it is very necessary that the ribs should be held down by contraction of the muscles passing between them and the pelvic girdle, otherwise the force of the contracting pectorales would merely elevate the ribs. Apparently the muscular components in this action have become stereotyped. Every time the pectorales act upon the arm, the muscles of the abdomen and loin spring to attention to anchor the lower ribs. They spring to attention, when we merely press the elbow downwards against the arm of the chair just as they would if we were about to haul ourselves up to the branch of a tree that we had grasped with our hands. Now when I sit at ease in my arm-chair I am in no likelihood of elevating my ribs when I make a minimal downward movement with the elbow; nevertheless, the abdominal muscles will contract on the supposition that their fixating rôle will be necessary—and I have no power to prevent their action.

If I wish to raise my arm from my side the deltoid muscle is the main agonist upon which I call to perform the act. The deltoid, acting from the bones of the shoulder girdle will pull the humerus upwards from the side of the body; but it can only pull it upwards until it is at right angles to the trunk, or at right angles to the scapula. If we wish to raise it still further so that we hold it vertically with the hand above the head, the action must be done by rotating the scapula. The humerus still remains at right angles to the scapula, held so by the deltoid, and then the scapula is rotated so that its lower angle swings outwards and the arm goes up. The muscle that we call upon as agonist to rotate the scapula is the serratus magnus which, acting from the ribs, sweeps the lower end of the scapula outwards towards the side of the chest (see Figure 64).

Now, in the first stage of the movement, when the deltoid is raising the arm from the scapula, it is obvious, since the scapula is not fixed, that the weight of the arm would readily rotate the scapula so that its lower angle moved inwards. Some muscle must be called upon as a synergic in order to prevent this undesired inward rotation of the scapula and so permit the deltoid to carry out the act of volition. The muscle that is called upon is the trapezius which, by its peculiar anatomical arrangement, can counteract inward rotation of the lower end of the scapula. If the fingers be placed over the lower angle of the scapula when the movement of the deltoid is initiated there will often be felt a

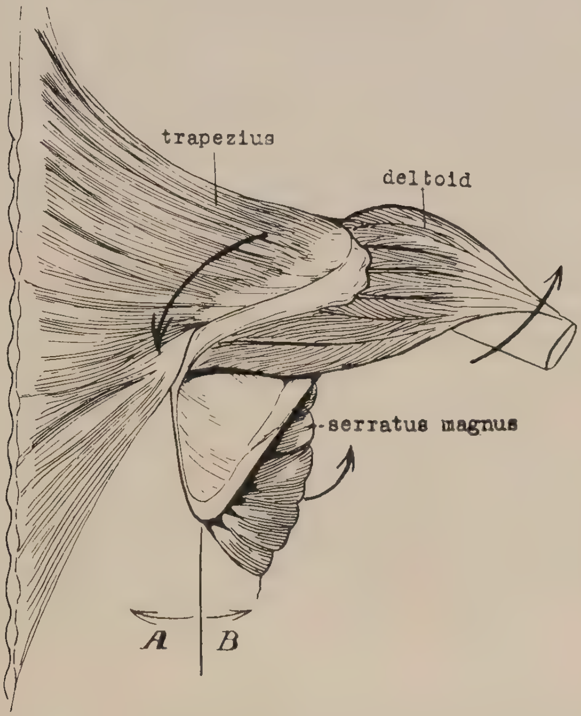


FIGURE 64.—Diagram to explain the action of muscles in elevation of the arm from the side of the body. A, direction in which the angle of the scapula moves when the arm is raised by the deltoid. B, direction in which it is moved by the action of the trapezius and serratus magnus.

curious movement, for the angle will first start to move inwards, then pause, and then start to move outwards. The pause marks the moment when the synergic action of the trapezius is called upon. When the trapezius has contracted as a synergic and steadied the scapula, and after the deltoid has exerted its full range of movement and raised the humerus at right angles with the scapula, the serratus magnus is called on as an agonist and the angle of the scapula begins to move outwards.

Now if the spinal accessory nerve be damaged and the trapezius is paralysed, a very curious thing happens. The deltoid acts, but as it acts the scapula, lacking the synergizing action of the trapezius, swings inwards. The deltoid can still move the humerus until it is at a right angle to the scapula, but, owing to the rotation of the scapula it is unable to raise it to a right angle from the side of the body. The serratus magnus begins to contract when the deltoid has done its utmost and swinging the scapula outwards, raises the arm to the level of the shoulder, by restoring the scapula to its normal position. The combined actions of the two agonists therefore achieve, in the absence of the synergic, the movement that could have been effected by one alone when acting with its synergic. Now the curious thing is that, since the serratus magnus is able to rotate the scapula outwards, it could, theoretically, perform the synergizing action for the deltoid, by acting simultaneously with that muscle. But in the ordered play of the components of the movement of raising the arm from the side the serratus magnus is allotted the rôle of an agonist, an agonist that is called upon to act after the deltoid has done its utmost in this capacity. It has not been given the rôle of synergic—that is the part of the trapezius—and when the trapezius is paralysed we are incapable of forcing this rôle upon it.

Perhaps an even more instructive case, and one of great practical importance, is that afforded by the surgical procedure of the tendon transplantation in cases of musculo-spiral paralysis. The musculo-spiral nerve supplies the muscles that extend the wrist and the digits.

If the nerve be irreparably damaged, so that its ends can never be joined by any surgical operation, the patient suffers from the disability that the wrist and fingers are permanently flexed and the wrist cannot be extended nor the fingers straightened out. Since there are now so many unopposed flexor muscles for the wrist and fingers some of these can be spared and by having their tendons brought from the front of the wrist to the back and then joined to the tendons of the paralysed extensors they may be made to pull upon them and so act as extensors although they belong to a flexor group. When this is done successfully the patient can extend his wrist and straighten out his fingers by the use of muscles that were originally flexors. There is a cortical volition to extend the wrist: there are muscles having the mechanical arrangement which makes this movement possible, and they are therefore called upon to perform it.

Now when we grasp an object with the hand we employ all the flexors of our fingers: but these finger flexors can also flex our wrists. In performing the action of grasping we, therefore, call upon the extensors of the wrist to act as synergics and so prevent the undesired wrist flexion. The more forcible the movement of grasping becomes the more forcibly the synergizing wrist extensors act: until, when great force is required in the grasp, as in lifting a heavy object from the ground, the wrist is involuntarily extended in order to give the flexors their maximum power. In the case of tendon transplantation that we have been considering, the patient can compel his old wrist flexors to play the rôle of agonists and so extend his wrist and fingers. His cortex can dictate the movement. But he can never compel his new extensors to act as synergics to his old flexors. When he flexes his fingers in order to grasp, his wrist flexes with his fingers and the force of his grasp is lost. He performs an unsynergized action. The cortex, since it may dictate movement, may dictate to the agonist but here its power ends: the other components in the complexity of skilled movements are regulated by something that is not cortical but something that is absolutely essential to the proper carrying out of even the simplest movement of a part.

CHAPTER XXXII

THE CEREBELLUM AND ITS PRIVATE PATH.

Few organs have been more misunderstood than has the cerebellum; and this is the more pity since in the complexity of its gross anatomical structure it is one of the most beautiful organs in the body. By a strange twist of fate it was to the researches of Gall and Spurzheim that, a century ago, neurologists owed some of the most important knowledge of the cerebellum: it was to the same two investigators that neurology owed that stultifying concept of cerebellar functions comprised in the doctrine that the cerebellum was the seat of the sexual impulses. It was a simple matter for the experimental physiologist to remove the cerebellum of a pigeon and to note that, though the bird's sexual impulses appeared to remain undisturbed, it was so gravely affected by the operation that it toppled over in a very definite and regular manner whenever it attempted to move. The cerebellum was dethroned from its high place as the controller of sexual life and was no more than part of the cerebral mechanism which especially functioned in preserving the balance of the body. But even in disposing thus of the functions of this remarkably complex portion of the brain there was but little satisfaction for the clinician, for cerebellar lesions were notoriously varied in their resultant symptoms and a loss of balance was certainly not always a dominant feature of human loss of cerebellar function. As with the cerebral cortex, so with the cerebellum, more may be learned from the study of its rise and its associations than from the tangled mass of experimental findings, instructive though these may be when their interpretation is properly carried out.

In the lower vertebrates the cerebellum is extremely small and, in its way, extremely simple. So small is it that its very existence, even in the Amphibia, has been denied by comparative anatomists: so simple that in its inception it is little more than a thickening of the dorsal margins of the fourth ventricle. The thickening of the wall of this particular portion of the medulla is, however, one of the most instructive facts concerning the cerebellum since here is the site of the instreaming fibres from those primitive proprioceptive organs comprised in the lateral line sensory mechanisms, which, as we have seen, are the earliest prototype of the labyrinthine system. In Chapter XXIX it was noted that the cerebellum was always begot in relation to the instreaming of silent proprioceptive fibres, and in the lowest vertebrates it is the labyrinthine system that provides the greatest source of these silent impulses.

Little by little in the evolutionary series the two lateral thickenings, which mark the origin of the cerebellum, meet above the central cavity of the medulla and so form a median organ situated in the roof of the fourth ventricle and connected with the nuclei developed as the head stations of the vestibular nerves. Such a cerebellum, characteristic of the lower vertebrates, would obviously appear to be a co-ordinating or correlating centre for those proprioceptive impulses that are derived from any type of labyrinthine system. But the labyrinthine system is not the sole source of proprioceptive impulses. As evolution proceeds, and especially as land-living animals come to support themselves upon their limbs, a new flood of silent informative stimuli streams inwards and demands place in their great silent receptor. Such impulses stream upwards by way of the spinal cord and force their way to the cerebellum and now, in addition to the vestibulo-cerebellar pathways, there is added the inception of the great spino-cerebellar paths. Such an increment of new pathways leads to further elaboration of the cerebellum as an anatomical structure and from being a comparatively trivial organ it assumes forms in some of the lower vertebrates that are extremely complex and difficult to classify upon any one general scheme. Nevertheless there is always in such a cerebellum a division of *vestibulo-cerebellum* (vermis and floccular lobes) that receives fibres direct from the vestibular nuclei, and a *spino-cerebellum* (dorsal and median portion of the vermis) that is connected with the upstreaming spino-cerebellar paths. Here then we have an organ that seems clearly to be related to the two main sources of proprioceptive stimuli; an organ built about the site of the instreaming impulses from the balancing system of the vestibular nerve and to which come, in land-living vertebrates, the silent messages from the joints and muscles of the limbs; an organ that clearly enough seems to be a co-ordinating centre for all those stimuli having to do with the orientation of the body and one related to its poise and balance. We would naturally expect, since a large animal must needs have a greater wealth of proprioceptive fibres running inwards from its bulky body, the cerebellum would increase in size and complexity merely in relation to body growth. This is an expectation that is fulfilled in all pre-mammalian vertebrates: the great afferent centre of proprioceptive impulses keeps pace with the growth of the areas from which proprioceptive impulses may stream. Its growth in bulk increases: but the complexity of its surface pattern appears to increase even more remarkably than the complexity of fissuration that we have previously noted in the cortex of the cerebral hemispheres: and this probably for the reason that, unlike the cerebral cortex, the cerebellar cortex does not increase greatly in cell complexity as the evolutionary story is unfolded. Throughout the fish, amphibia, reptiles and even the birds the cerebellum is an organ such as we have pictured. It is a head station for vestibular and spinal silent impulses: it is an organ dealing mainly with bodily poise and with the function of orientation in space. It has therefore, at this stage of development, been termed the *paleo-cerebellum* or the *paleo-static system*. It matters little what we name it: it is essentially a cerebellum developed to such a stage as is possible in a vertebrate type in which the pallium is comparatively unimportant and in which, therefore, pallial influences cannot be brought to bear upon cerebellar function.

We have seen that when the pallium became a factor in the ordering of movements of the body it largely usurped the functions of those parts of the brain that had conducted the business before it rose to importance. With the cerebellum the case is, however, very different. The advent of pallial movement was the death blow of the striatal system: it added new glories to the functional rôle of the cerebellum. It was Gall and Spurzheim who first clearly pointed out the great distinctions of the mammalian cerebellum. It was they who showed how vastly it exceeded that of the pre-mammalian vertebrates in complexity. Varolius may have described the Pons: but Gall and Spurzheim first clearly claimed it as a mammalian distinction and shrewdly concluded that its relation to the hemispheres of the cerebellum was such as the corpus callosum bore to the hemispheres of the cerebrum. In mammals the cerebellum makes great advances: and it is true to say that pallial development and cerebellar development go hand in hand. More than this, it is true to say that with increase in the usurpation of striatal functions by the pallium, the cerebellum grows in size, complexity and importance. This distinctive mammalian development does not consist merely in an enlargement of such an organ as was seen in the pre-mammalian vertebrates, for new parts are added to the old cerebellum (see Figure 65). Between the vermis and the flocculus of the paleocerebellum is an area, which Elliot Smith has well termed the area crescens, that is typically mammalian in its growth and elaboration. It is the growth of this area which, forcing the flocculus and vermis apart, constitutes the dominant portion of the two typical mammalian cerebellar hemispheres: it is the formation of these two hemispheres which finds its expression in the development of that great band of commissural fibres that constitutes the *Pons Varolii* (see Figure 55). The mammalian cerebellum is distinguished in all this: it develops the typical lateral cerebellar lobes, it develops a pons, its area crescens dominates its vermis and its flocculus, as the non-olfactory pallium dominated the old olfactory cortex. It is the cerebellum of the Primates and especially the cerebellum of man that shows the perfection of its evolution. Here again is unfolded the same story—the story of arboreal life, of the freedom of the sensitive hand, of binocular stereoscopic vision—and the attainment of that wide range of highly skilled movements, which typical of our phylum, culminates so triumphantly in us. Until the mammalian stage was reached the vestibulo-cerebellar and the spino-cerebellar pathways constituted practically the sole connections of the old cerebellum: with the earliest mammals there comes the all-important accession of pathways from the pallium.

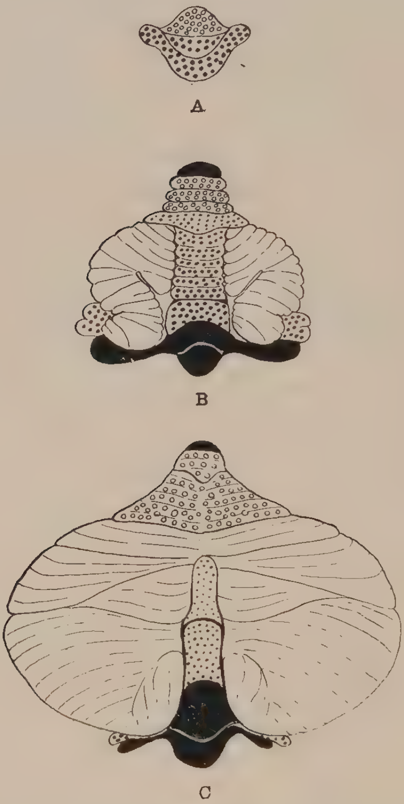


Figure 65.—Diagrams of the cerebellum of A, a reptile. B, a typical mammal. C, man. The parts marked black are the old vestibular portions: those left white are in connection with the cortex. (Founded on the work of Ingvar.)

It is the cortico-cerebellar pathways that make passage to the area crescens and to the lateral lobes and their nuclei: it is the cortico-cerebellar pathways that add the new and dominant functions to the rôle of the cerebellar cortex.

In addition to the vestibulo-cerebellum and the spino-cerebellum there is now a cortico-cerebellum, or a *neo-cerebellum* or a *neo-static system.*

We have seen how complex a thing is a skilled movement dictated by the pallium: we have seen the limitations of the pallium in ordering all the details of that movement. Agonists, antagonists, synergics and fixators all have to play their part: and the cortex is concerned solely with the agonists. By the old vestibular paths, by the cerebello-spinal paths and by the cortico-cerebellar paths the cerebellum is in receipt of all those impulses which are concerned in carrying out the elaborate details underlying the complexity of a movement dictated by the pallium. The great silent paths of the posterior columns of the spinal cord that in Chapter XVIII we traced to the nuclei gracilis and cuneatus and so to the decussating fillet, tell the cerebellum of the disposition of the body. The cerebellum is truly, as Sherrington said, "the head ganglion of the proprioceptive system," and as such is the mechanism that co-ordinates all the factors necessary in the performance of a skilled movement. It is the cerebellum that is responsible for the antagonists, the syner-

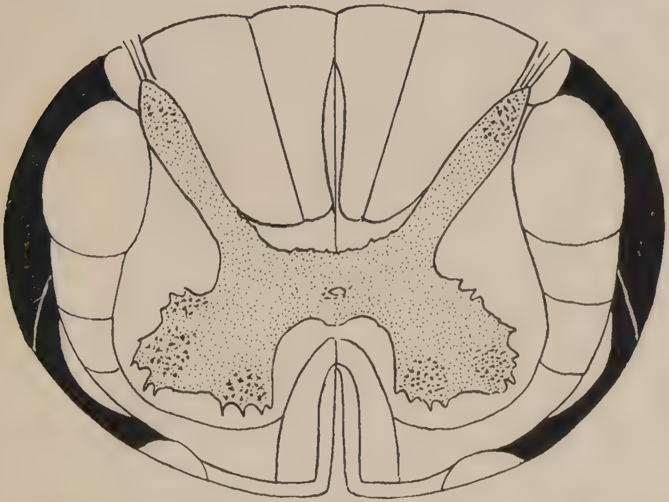


FIGURE 66.—Diagrammatic section through the spinal cord to show the spinal tracts. The cerebellar pathways are black.

gics and the fixators: it is the cerebellum that causes the cortical volition for movement to be promptly obeyed and properly carried out. It is the cerebellum that does what the pallium cannot do in movement: and it is all done without the intervention of consciousness.

Now, if the cerebellar influence be removed from the lower motor neuron the upset of the mechanism of movement is well marked. In man, lesions of the cerebellum entail no disturbance of sensation, nor do they produce loss of equilibrium as such. There is one effect of all cerebellar lesions, which probably underlies all the symptoms, and which is best termed *Asynergia*. By asynergia is meant a dissociation of movement into its elements, by reason of the failure of the accurate combination of the rôles of agonists, antagonists, synergics and fixators. It is this asynergia that produces the slowness and uncertainty of movement: a slowness of starting and stopping, and a feebleness of the whole action that is termed asthenia. It produces a clumsiness, an irregularity, and a tremor of movement known as astasia: and the muscles exhibit a curious weakness that constitutes one type of atonia.

Even in the movements necessary to produce speech it is manifest in the production of a typical scanning of the words uttered, and in the movements of the eyes it shows itself in the production of nystagmus of a definite type.

The cerebellum does not initiate movement: throughout the vertebrates it is electrically inexcitable: but it is dominant in movement in that it weaves all the elements into one harmonious entity in performing an action such as the pallium dictates.

CHAPTER XXXIII

CHANGES IN LEVEL

Sensation and movement, those great evidences of life which are of such paramount importance to all living animals, have undergone many strange transformations in the animal series.

Sensation is not always of the same quality and movement is not always of the same nature. When we speak of a lowly vertebrate as feeling something we do not necessarily mean that it receives or interprets a sensory stimulus as we do; and when we speak of it as moving we do not mean that the initiation of the movement and the circumstances of the movement are as they are in ourselves. There are differences in the quality of sensation and movement, and these differences are mainly centred in the *levels* of their receipt and initiation. By the convenient term levels is meant that a function may be represented in and discharged from various seats in the central nervous system. A sensory or motor phenomenon may have its mechanism of receipt and discharge in, say, the spinal cord, in the neurobiotaxically grouped nerve centres of some part of the brain stem, or in the pallium itself. We may say roughly that there are three levels, the level of the spinal cord, the level of the sub-cortical ganglionic masses of the brain stem, and the cortical level of the pallium or mantle.

Sensation and movement have found their representation at all these levels. The simplest circuit by which sensation can be received and movement can be initiated is by the synapse between the dendrons of the lowest sensory neuraxon and the motor cell in the anterior horn of the spinal cord which is the parent of the lower motor neuron. In this circuit the stimulus received from the terminal sense organ passes along a sensory nerve—the neuraxon of a posterior root ganglion cell—to the posterior column of the spinal cord: it then passes by dendronic synapses to the motor nerve cells in the anterior horn of grey matter of the spinal cord and so through motor nerves to the muscles. Such a circuit is the anatomical basis of what is functionally a pure reflex. We may say, in general terms, that the animal does not necessarily feel the stimulus for though feeling may normally be associated with the stimulus it is not essential to the reflex action: nor does it dictate the response. The response is preordained and inevitable, since it depends upon the dendronic linkages between the incoming sensory nerves and the ganglion cells of the issuing motor nerves.

If we cut off the head of an eel the creature will wriggle actively and all the movements of a normal eel will be rehearsed in the absence of any part of the brain. A decapitated snake or a decapitated bird will carry out active movements for a considerable time after the decapitation. Here the whole of the movements, complex though they may be, are initiated from the motor anterior horn cells of the spinal cord. The eel and the snake wriggle, the bird may run or even fly, but the whole mechanism by which they carry out these activities is reflex. The animal does not feel the stimulus nor dictate the response. A man with a lesion of the spinal cord may retain certain reflexes. Human reflexes in cases of complete section of the spinal cord are limited, nevertheless they are instructive. When a stimulus is applied to the sole of the foot or to any part of the leg there is carried out a complex reflex that consists in flexion of the hip, adduction of the thigh, flexion of the knee and an upturning of the foot and the toes. This is obviously a complicated combined movement and one that is purposive since it is aimed at withdrawing the parts from the noxious stimulus. It is a reflex of protection: a defensive mechanism of the most primitive kind. An extension of this combined automatic action may be evoked by scratching the limb, and in this larger manifestation, or "mass reflex," there is, in addition to the withdrawal of the legs, a contraction of the abdominal muscles and an emptying of the bladder and at times the rectum. Here again is a complicated yet purposive spinal reflex co-ordinated to serve the primitive function of excretion. In addition to these are the spinal reflexes obviously designed to carry on the movements involved in the processes of reproduction. Cremasteric, dartos, and bulbocavernous reflexes result from stimulation of the male genital organ and they may culminate in that far more complex co-ordinated movement in which the muscles of the legs and abdomen take part and, which has been termed by Riddoch the coitus reflex.

In man, as in all higher mammals, the spinal cord reflexes are, however, limited when comparison is made with the lower vertebrates. They are all transacted without the intervention of the conscious will of the patient. Lowest level—or spinal—receipt and translation of stimuli is, therefore, something which, though dominant in lower vertebrates, has been supplanted in higher vertebrates by the translation of the function to higher levels in the central nervous system. In a spinal cord level of sensory receipt and motor outflow there is no question of feeling or appreciation of the stimulus. The human patient does not know that he has been touched, he does not know that his legs have moved. Something flows in and something flows out, but the higher centres are not necessarily informed.

Next in the phylogenetic story there comes about the translation of these lowest or spinal cord co-ordinations to a higher level. There are first of all the crude affective stimuli which stream in from the anterior end of the body and which are mostly concerned with the sensations that are related to the perception of substances that may possibly be utilized as food. Stimuli received by the anterior sense organs may be pleasant or unpleasant; they may inform the animal that the object encountered is suitable as food or is noxious. The sense organs are, to use a much-overworked word, exteroceptors. These sense organs are linked to the brain stem and in the brain stem they find their primitive cell stations in the ganglionic mass known as the thalamus. To the primitive vertebrate thalamus there stream the impulses derived from those anterior testing placodes that are primarily related with the getting of food. We may term the sensory impulses olfactory, sampling or first cranial nerve impressions, it does not matter what term we use, only is it essential to remember that they are sensations that are mainly concerned with the obtaining of food. The primitive thalamus, which is the cell station for these crude, affective, impulses concerned with the search for food, has alongside it, in neurobiotactic harmony, a primitive executive or motor nucleus —the corpus striatum—from which there are initiated motor impulses that are primarily connected with the getting of food. The primitive thalamus then takes the place of the posterior root ganglion cell and the primitive striatum of the anterior horn spinal cell. Although these second-level stations are at first dominantly connected with the stimuli and responses involved in obtaining food, they gradually become the centres for the receipt of other impulses and for the transmission of other motor responses. They take over very completely, and far more efficiently, the functions that were formerly lodged in the spinal cord. Both thalamus and striatum become increasingly complex by the addition of new ganglionic masses in the phylogeny of the vetebrates, and in both bodies there is an old part, concerned mainly with food-getting activities and a new part concerned with wider bodily adjustments. There may be said to be a *paleothalamus* and a *neothalamus*: a *paleostriatum* and a *neostriatum*. The thalamus now becomes the great receptor for all the more crudely affective or protopathic sensations from the whole of the body and the striatum becomes the great executive for the motor responses of these affective stimuli. This mechanism is the effective sensori-motor apparatus of all the lower mammals. Their stimuli are thalamic stimuli; their responses are striatal responses.

From analogy, we are probably justified in imagining that the stimuli are of crudely affective, protopathic type and that the response is essentially a reflex, though it may express itself as highly complex instinctive behaviour. If a lower mammal be deprived of its pallium it may still receive stimuli and initiate movement; its pallium, as far as sensation and movement are concerned, is a luxury rather than a necessity. Moreover in the marsupials, although movements may be evoked by electrical stimulation of the cortex, they may also be produced by stimulation of the striatum. In mammals higher than the marsupials, the striatum ceases to be excitable by electrical stimulation though it still functions as the dominant motor initiator. If a mammal, such as a rat or a rabbit or a dog, has the whole of its electrically excitable or motor cortex removed it may still carry out all its habitual body movements, for the subcortical thalamus receives the stimuli and the subcortical striatum initiates the impulses for movement. But if a dog be deprived of its cortex and its striatum it at once becomes inert. It can stand and walk, but will only do so as the result of stimuli, internal or external. It runs into any obstacle and finally lies down until a new stimulus arouses it. It will not seek food and would die unless food were placed in its mouth. A dog still possesses some of its spinal cord or lowest-level adjustments of sensation and movement, but not enough to preserve its life unless artificial means of keeping it alive are employed. It can get along without its sensory and motor cortex—which are super-added luxuries in the attainment of co-ordinated responses to the environment; but its second, level centres—the receptive thalamus and the executive striatum—are essentials. Nevertheless although a dog depends upon its thalamo-striate mechanism as its highest-level sensori-motor apparatus it does possess a pallial area which is capable of producing motor responses when electrically excited. The possession of this area we have described as more or less a luxury, yet we may be confident that when this area is destroyed in a dog, there is something lacking in responsive behaviour, even though it may be difficult to detect some time after the infliction of the injury.

Through the ascending sequence of cerebral development in the mammalian phylum the story seems to be clearly told. In the lower Primates some loss of movement results from destruction of the area of pallial motor excitability, and though this may be recovered it is sufficiently definite to warrant the assertion that, in the monkeys, there is a pallial, or supra-thalamic, or third-level representation of sensation and a pallial or supra-striatal, representation of movement.

In the anthropoid apes the pallial areas are of still greater importance, and a wider and more permanent paralysis (especially of the fine movements of the hand) is produced by destruction of the electrically excitable cortex.

In man we have a fair knowledge of the translation of sensory impressions from the thalamus, and of the initiation of movement from the striatum, to the pallium. In us, our discriminative actions, which concern those parts of the body of which we are cortically aware as entities projected in space, are initiated from the cortex; for the cortex has very fully usurped the initiatory functions of the striatum. In us, the discriminative spatial awareness of our bodies is a function of our sensory pallium—only the crudely affective sensations still find thalamic rerepresentation. Sensation, of a very definite quality, and movement of a very definite type, have, therefore, in man been removed from the second-level station to the third-level station in the cortex. It is this translation that secures for man his very basis of humanity, since human deliberative conduct—the outcome of discriminative stimuli and of response called forth by his awareness—constitutes a complex different altogether from the habits, instincts or reflexes of the lower mammals.

CHAPTER XXXIV

MOVEMENT AND EDUCATION

If we are to arrive at any understanding concerning the mechanism of even the most ordinary movements of our fellow-men, we must for ever bear in mind the fact that human movement is a thing widely different from animal movement.

Human movement has been raised to a cortical level, but it is only in certain of the lower animals and only under special conditions that movements are initiated at this high plane.

The great thalamo-striate complex is replaced and repressed by the cortex in man in a way that does not happen in other animals. Without attempting to pass off words as token for real knowledge, we may say that instinctive movement has been replaced in us by deliberative considered movement. The change affects the level of initiation—it does not alter the type of movement. An animal may perform a certain movement, which is in all its essentials the pure outcome of, what is called, instinct: a man may produce a similar movement, but in its production there is no factor to which the word instinct could possibly be applied. When we come to realize the considered and purposive character of most of our own movements we are very likely to be led into believing that a similar deliberative purpose lies behind the similar movements of lower animals. Observations upon animal behaviour always need to be carefully reviewed when inferences are drawn regarding the apparent deliberative nature of a movement, the performance of which by us would certainly indicate deliberate and considered purpose, but which, in the animal under observation, may be no more than an unconsidered and instinctive action. There is unfortunately a class of nature lover's literature that ignores entirely this consideration of the level of initiation of movement and does not hesitate to read human purposive motives into the most crudely reflex and instinctive movements of mammals, birds and even insects.

It is also easy to be deceived as to the apparently instinctive or reflex nature of certain human actions, and as this is an error more serious than that of assigning cortical deliberation to the movements of lower animals, the subject may be discussed in more detail.

We have seen that by neurobiotaxis there is brought about that grouping of the nerve cells in the brain that ensures such a mechanism as the suckling reflex. A new-born pup, a blind kitten, a human baby are all alike in this—they possess the neuromuscular mechanism, all properly linked up before birth, that produces the instinctive movements of the lips, tongue and throat when the nipple comes into contact with the lips. A human baby no more learns to suckle than does a puppy. But a human child may educate this complex movement of sucking and raise the level of its initiation so that it becomes a highly deliberative act. It may learn to suck an orange or a tobacco pipe, and in the proper regulating of the suction of a pipe there is a considerable demand upon considered movement and a marked condition of awareness of all the parts involved in the action. But a human baby has not many elaborate instinctive movements at its command: most of its accomplishments must be learned from the beginning.

Many young animals are very helpless at birth; but their helplessness is different in its nature from the helplessness of the human baby. A new-born rabbit does not walk, but it fails in this function, not because it has not yet learned to walk, but because, being one of a large family and born in the safety of a burrow, it is blind and singularly immature. A young hare, born in the open and, maybe, a solitary offspring, can manage the business of walking at once, not because it learns to walk more readily, but because its eyes are open and the muscles, bones, joints and nerves of its legs are in a more complete state of development. Young animals do not have to learn to walk, since in them the movements of walking are not initiated from the cortex but from the striatum: human babies have to learn to walk because walking being a pallial function, and the pallium being educable, some education is necessary before the art can be acquired. Babies that are deficient in cortical development do not learn to walk at the proper time, and every baby has to undergo a long apprenticeship before the difficult business is thoroughly mastered. The fact that a human baby has to educate its cortex in learning to walk is often lost sight of, for it is easy to assume that the business is more difficult for the human baby than it is for a foal or a calf since it has to balance itself upon its two feet and walk upright. It is, however, not the business of standing upright that is the difficulty; it is the education of the cortex in performing the act of walking. The young of the upright kangaroo has no more difficulty to encounter than have the young of any typically pronograde four footed mammals. The young kangaroo performs all the movements of walking instinctively or reflexly and initiates them from below the level of the cortex. Its cortex is not involved in the matter and it even lacks that great nerve pathway—the pyramidal tract—which alone could carry impulses from its cortex to the muscles of its legs. The human baby is born with only enough of these instinctive or reflex mechanisms to ensure its life during its period of helplessness—all other muscular performances must be learned, since they are cortical in origin. The life of a developing infant is crowded with education, it is learning new movements every day. Every day cortical awareness of its limbs is becoming more vivid and every day it is learning to dictate movements of those parts of which it is becoming aware. It learns to crawl; it learns to walk; it learns to run; even it may learn to dance and do a hundred strange movements useful or useless. Every one of these accomplishments is learned as arithmetic or geography are learned, for all of them are the results of cortical education. A human infant's development of muscular movements is a story of cortical education: a young rabbit's development of muscular movements is a story of perfecting muscles and the laying down of neuromuscular pathways for the perfection and elaboration of subcortical reflexes. It is a common observation that the lower mammals can swim instinctively. A cat, which is not a water-loving animal, may be thrown into the water, and, even if it be its first experience, it will swim with great apparent skill. The rôle of the cortex is remarkably well shown in the difficulties with which some human beings acquire the art of swimming. Cortical knowledge begets apprehension of drowning, and leads to an appreciation of the improbability of success in performing the feat of swimming. The rhythmical movements are easy to accomplish, but to adapt these rhythmical movements to the business of keeping afloat and making passage through the water is a thing which many find great difficulty in attaining. It is a common experience of those learning to swim that one day they realize that the thing is possible, and having attained the cortical knowledge that they are able to swim, they may perfect themselves in the art and educate their movements. Having reached this stage of a cortex educated to realize the possibility of the feat and to perfect the movements necessary to accomplish it, the whole thing is done. The pupil may become a better swimmer by further education of his movements, but he will never again be unable to swim—his cortex has been educated to it.

It is said that practice makes perfect; and indeed the thing is very true, but it is even more true to say that if practice may not ultimately produce perfection it will always make the doing of the action more easy. It may even make it suspiciously easy. Playing the piano, using the typewriter, knitting and the vast series of mechanical, repetitive, manual occupations all become so easy that practice seems to have made them almost reflex in their mechanism. There are even now exponents of that mediaeval type of philosophy which revelled in the use of words such as *mind*, *consciousness*, *reflex*, and many others and used these words as talismans therewith to solve all questions of human behaviour. Such words are dangerous things even when they are used with strict regard to such cerebral functions as can be correlated with cerebral structures; but when they are used in an abstract fashion and in the absence of any knowledge of comparative neurology they have nothing whatever to recommend them.

With philosophers of this school, as a dogma, and with many who do not trouble to think, as a substitute for thought, there is a belief that when repetitive actions become so suspiciously easy it is because their initiation is relegated to a lower level of mind or consciousness or what-not.

Though it may be appreciated that in learning to walk a human baby is educating its cortex, it is often assumed that once the actions of walking have been mastered and the thing becomes automatic or reflex or unconscious it is carried on, not from the cortex, but from some lower centre.

Here the proverb shows more wisdom than the philosopher. It is practice that makes perfect; but not practice that determines the removal of the business of initiation from the cortex to a lower level. All the neurological evidence available goes to show that every movement that becomes what may be termed automatic by repetition is facilitated at the level of its first initiation, it is not carried out at any lower level. And indeed were one to regard the matter as the philosopher, in an abstract way and divorced from evidence, it would seem an idle thing to educate one nervous mechanism and, when its education was completed, to put it out of the business in favour of some other mechanism. But apart from such speculations there are the well-known facts derived from experiment and from clinical observations. Walking in all of us is a cortical function and an injury to the cortex will put a stop to its manifestation. No matter how automatic or reflex walking may appear, its easy accomplishment in the adult is merely the outcome of facilitation at the cortical level: it is never carried on by the striatum, by the cord or by any other nerve centre. Cut the internal capsule and the power to walk ceases. Nor is this surprising; for if we reflect on the subject we will surely realize that even in the most routine type of walking along a paved street, we have a great consciousness in the business though we may think of many things as we walk along. There are not many among us who have no regard for paving stones. Though we may be absorbed in reflections concerning relativity or the payment of our debts, most of us have a care for walking on the middle of the flag-stones or on the cracks that separate them. Most of us arrange some way ahead which foot it shall be that steps down from the path when we come to the corner: and others have more elaborate cortical awareness of the business of walking than that.

CHAPTER XXXV

THE BRAIN AND THE HIND LIMB

In the pantomime elephant the actor who plays the rôle of the hind legs has to make his gait fit in as best he can with that of the actor playing the part of the forelegs. Herein lies the art of acting as an elephant's hind legs. The man in front can manage the manipulation of the trunk and ears and he can dictate the movements of the whole animal; the man behind has to harmonize his actions as best he can. Strange though it may seem the pantomime elephant is not so very outlandish in this respect; even nature seems inclined to leave the hind legs to look after themselves and to take their cue from the fore-limbs, and in the lower mammals to let the head and neck dictate to the whole. In the typical mammal the position of the head in space can determine the position of all the limbs and this by virtue of the fact that within the head is lodged the labyrinthine spirit-level system and to this spirit-level system come the proprioceptive stimuli from the neck.

Both the stimuli from the labyrinthine system itself and the stimuli derived from the muscles of the neck, inform the brain of the orientation of the head in space. This information provides a stimulus which reflexly reacts upon the muscles of the limbs and causes them to assume an appropriate attitude in preparation for a movement.

If an animal has the whole of its fore brain destroyed so that pallial influences are prohibited from taking any part in its subsequent movements, the labyrinthine influences are still definitely displayed in limb posture. If the head of such an animal is elevated, so that its nose points upwards, then its fore-limbs will extend whilst its hind limbs flex. This is a reflex action which has as its apparent object the preparation for an upward movement of the whole animal in response to the elevation of its head.

If, on the other hand, the head is depressed so that the nose is pointing downwards, then the fore-limbs flex whilst the hind limbs extend. If the lower part of its neck is depressed so that the head and neck lie flat, then all four limbs flex and the animal squats flat upon the ground. The labyrinthine system is all-important in the lower animals but its influence in man, as we have seen, is comparatively trivial. In man the eyes tend to usurp the functions of the labyrinthine system, for man obtains his impressions of orientation mostly by visual stimuli, and these stimuli are translated to the level of the pallium. Yet, even in the lower animals, there is a peculiarity that has been noted by Rudolph Magnus, the pioneer, in unravelling the complexity of these reactions. From his numerous experiments upon animals he has shown the vast importance of labyrinthine impulses: but he has also been forced to the conclusion that "head movements have a very strong influence on the fore-limbs, whereas the reaction of the hind limbs is much weaker." Evidently even with this primitive mechanism for the control of posture and movement the hind limbs do not get their full share of the central influence. They have to look after themselves by virtue of lower connections and their own proprioceptive stimuli. When the elephant's head moves, it may reflexly send very emphatic messages to its limbs, but it appeals far more forcibly and directly to its front legs than to its hind legs. The same story is repeated with every change in initiating mechanism and with none is the lesson more clearly expressed than in the transition to pallial control of movement. We have seen that the cortico-spinal tract, the great pathway from the pallium to the motor nerves of the lower motor neuron, ends in the lowest mammals in the brain stem: so that, although the cortex controls the movements of the head, the movements of the limbs and trunk are regulated by lower centres. We have also seen how, in the ascending phylum of the mammals, this tract extends further and further back along the spinal cord and so brings cortical influence to bear upon the movements of the neck, the shoulder, the fore-limbs, the trunk and finally, in us, upon the hind limbs. Even in man there is evidenced the far greater power of recovery of leg movements than of arm movements when the cortex or the cortico-spinal tracts are damaged. Now in such mammals as the marsupials and the lowest monodelphians the cortico-spinal tracts bring cortical influences to bear only on the fore-limbs, for the extension of the tracts to the lower motor neurons of the hind limbs has not been developed. The cortex can, therefore, dictate to and initiate movements in the fore-limbs, but the real elephant is in this regard much like its stage counterpart, for its hind legs must get on as best they can by the use of some other mechanism. Bearing this anatomical fact in mind there are some interesting features of animal movement to be noted and these perhaps have not received sufficient attention from students of biology. The pallial control of the fore-limbs naturally confers upon them a far wider range of movement and a greater independence and freedom of movement. The cortex can suggest a variety of uses for the fore-limbs: but the hind limbs will lag behind, both in the range and in the independence of the actions that they perform. The fore-limbs are the handmaidens of the brain, the hind limbs are the machines which are regulated to play their more lowly rôle in a reflex fashion. The lack of independent movement in the hind limbs of the lower mammals is a very striking fact. The majority of the marsupials, the more lowly insectivores, and the more primitive rodents all have this in common, that in ordinary progression, although the fore-limbs move alternately, the hind limbs move synchronously. If a generalized marsupial, such as a Bandicoot (*Perameles*) be watched in its normal slow gait, as it moves about in search of food, it will be noticed that first one fore-limb is advanced and then the other, and then both hind limbs come forward simultaneously. But when its speed is increased in its ordinary business of travelling it settles down into a regular gallop and both fore-limbs and both hind limbs move synchronously. Very much the same type of movement is seen in many rodents, and it is an interesting fact that Magnus found that in the rabbit the limb reactions following upon labyrinthine stimulation, due to head movements, differed from those evinced by cats and other animals with which he experimented. In the words of Magnus, "In all mammals, with the exception of the rabbit, movement of the head in different directions is followed by opposite reaction of one pair of limbs as compared with the other." Whereas, "In rabbits dorsiflexion of the head causes extension of all four limbs and ventroflexion of the head causes flexion of all limbs." It is by no means improbable that this curious distinction of the rabbit among laboratory animals is due to the fact that its limbs are employed synchronously in its peculiar hopping gait and not alternately as are the limbs of cats and dogs and other animals upon which these experiments have been performed.

As a development from the condition of synchronous movement of the hind limbs, comes that curious development of crural elongation, seen alike in marsupials, insectivores and rodents, that produces the typical saltatory mammal. The kangaroos (*Macropus*, etc.), the jumping shrews (*Macroscelides*), the jerboas (*Dipus*) and the jerboa mice (*Notomys*, etc.) are all examples of this development. In a truly saltatory animal, such as a kangaroo, the fore-limbs move alternately and the hind limbs synchronously in the slow progression of grazing. It is at the moment when the two hind limbs are moving forwards together in slow progression that the tail of the kangaroo is employed as a rest. When the animal progresses at any speed the fore-limbs cease to be employed, the tail is raised from the ground and the hind limbs act synchronously. There have been many explanations given for the development of a saltatory habit. The business of hopping and jumping has been said to be developed to enable the animal to leap over obstacles or to dodge more effectively in escaping from enemies, such as birds of prey. Neither of these explanations is in the least adequate. Jumping animals do not leap over objects in their path. If a stick be placed across a wallaby's run, no higher than a foot from the ground, the animal will inevitably go under the stick and not jump over it. Jumping marsupials (*Antechinomys*) and jumping rodents (*Notomys*) live in the open arid regions of Australia side by side with marsupials (*Dasycercus*, etc.) and rodents (*Pseudomys*) which do not leap; both forms are exposed to the same conditions, both have the same enemies, and the saltatory habit appears to have no special preservation value. The elongated hind limbs and this evolution of a saltatory habit would seem to be the natural result of the development of speed in an animal whose hind limbs had remained so little individualized in the mechanism of progression as to be capable only of combined synchronous movement.

It is to be noted, however, that in all saltatory animals so far observed, the hind limbs, though committed to simultaneous movement in progression, are yet capable of individual movement provided the proper stimulus is given. This stimulus is furnished by the well-known scratching reflex; when this reflex is excited the appropriate pes is brought into use with a perfect individuality of movement: an itch on the right side of the body brings the right hind leg into play: but in all other movements the right and left limbs act in unison.

Even when the hind limbs have attained an individuality of movement, we must remember that in many mammals they are beyond the reach of the cortico-spinal tracts. They are still beyond the control of the cortex, and their movements are, therefore, not voluntary. No previous awareness of their projection in space is involved in their movement. It follows, therefore, that in some mammals the fore-limbs may be subject to cortical control whereas the hind limbs, though moving alternately, act by a subcortical reflex mechanism.

When driving behind a horse, or better still a camel, provided with blinkers, a very beautiful phenomenon may be observed. If an obstacle lies directly in the animal's path it will raise its fore-foot high enough to step over it. This action is obviously the outcome of a visual impression, a cortical judgment and a cortically dictated movement. But once the animal has stepped over the obstacle with its fore-foot, the object passes beyond its range of vision. A camel wearing blinkers cannot see anything except the field of vision immediately in front of it. Nevertheless the hind foot is lifted from the ground as carefully as the fore-foot was, and with the same precision the obstacle is cleared. Both obstacle and hind limb are without the camel's visual field. Obviously in this there is some underlying mechanism which permits the action to be performed in the absence of a visual stimulus and even in the absence of a pallial initiation of the very specialized action. If an ungulate be watched as it progresses in an ordinary slow gait it will be noticed that the hind foot steps practically upon the spot that the fore-foot has just vacated. The movement of the hind limb, no matter if the gait be that of a camel or that of a horse, is practically a repetition of the movement of the fore-limb in as far as it traverses the same area and rests upon the earth in the same spot. If an object is not stepped upon by the fore-foot, it will escape the hind foot, for the one trod where the other will tread. The biologist who is given to the solution of mechanical problems might formulate a law of animal structure, by which the length of fore and hind limbs, the position of their joints, the range of their movement and their separation, as evidenced by the intervening length of the vertebral column, must be so correlated that the hind limb shall repeat the movements of the fore-limb. Such a law would seem to prevail at least among the ungulates and to be an outcome of the phenomenon of lack of pallial influence in the movement of the hind limb. In some horses the business is overdone and as the hind hoof comes forwards it not only occupies the spot formerly occupied by the fore-hoof, but it hits the fore-hoof even before it has left the ground. Since the mechanical build of the ungulate will insure the hind foot not stepping on an object which the fore-foot has avoided, all that is needed to account for the action of the camel in blinkers, is for the hind limb to be reflexly influenced by the action of the fore-limb. With such a reflex mechanism, the act of raising the fore-foot over an obstacle would be repeated when the hind foot came into action.

Truly the elephant can know little of its hind legs, since it cannot turn its head to see them and it even has to suckle its baby at axillary mammary glands in order to keep its eye and its trunk upon it. Yet the elephant that has stepped clear of the Hindoo baby with its fore-foot is in no danger of stepping on it with its hind foot.

CHAPTER XXXVI

THE LOWER MOTOR NEURON

It is the fate of every fibre of the cortico-spinal tract that it comes to an end by forming a synapse about a motor cell in the anterior horn of the spinal cord. It is this anterior horn cell that is the parent of the next link in the conducting chain for motor impulses. The anterior horn cell gives off a long neuraxon which, running as one element in a motor, or a mixed sensory and motor, peripheral nerve, ends in a motor terminal upon some muscle fibre. The anterior horn cell and its long neuraxon constitute the *lower motor neuron.*

As we have already seen, the anterior horn cell, before it gives off its long neuraxon, is brought into connection with dendrons from the lowest sensory neuron and so its first and lowest-level activities are catered for, and spinal reflexes are made possible.

Now the upper motor neuron segment constitutes a complex, for it contains four private paths—the cortico-spinal, vestibulo-spinal, striato-spinal and cerebello-spinal tracts—and the influence of all these privates paths is brought to bear upon the parent cell of the lower motor neuron. The lower motor neuron is, therefore, a common path conveying to the muscles the impulses for initiation of movement from the pallium, for the balancing of movement from the labyrinth, for the steadying of movement from the striatum and for the synergizing of the movement from the cerebellum. A welter of impulses traverses the lower motor neuron and all are necessary for the proper performance of even the simplest movement. It is usual to say that the lower motor neuraxons are gathered together and are distributed to the muscles as motor nerves or as the motor fibres in mixed nerves, and by the term motor nerves we generally imply that a peripheral nerve is an efferent mechanism consisting of a bundle of lower motor neuraxons. But in this sense there is no such thing as a motor nerve in the body. If a nerve has no more apparent office than that of supplying a definite muscle or set of muscles with activating impulses it is never composed entirely of lower motor neuron fibres. Even a nerve such as the hypoglossal, which supplies the muscle of the tongue, has in its composition many fibres which make their connection with sensory rather than with motor nuclei. Nerves which are termed purely motor may be said to have from one-third to one-half of their total bulk of fibres connected with posterior root ganglion cells or their equivalents. It is obvious, therefore, that lower motor neuron fibres form only one constituent of even the most typically motor nerves, and that each so-called motor nerve is largely afferent in function. That this should be so is a thing very easy to understand when we consider how much the muscle has to tell the higher centres before the mixed impulses of the upper motor neuron are brought to bear upon the lower motor neuraxons that activate and regulate its movement.

When the upper motor neuron is interrupted in its course there is produced a very definite result; a paralysis the peculiarities of which are familiar to us in the picture typical of upper motor neuron paralysis. When the lower motor neuron is interrupted a very different result is produced.

A muscle deprived of its lower motor neuron becomes a dead thing. It is truly paralysed and cannot act in any capacity. It becomes flaccid. It ceases to respond to electrical stimulation by the faradic current, its responses to the galvanic current become more and more sluggish in character and smaller and smaller in degree. Finally it ceases to respond to any form of stimulation, its structure degenerates, and as a muscle it ceases to exist. When the lower motor neuron and the lowest sensory neuron, combined in a mixed peripheral nerve, are severed in their continuity the loss of function is immediate, the muscles become paralysed and the part becomes insensitive: but it must be remembered that the muscles do not lose their faradic response immediately the nerve is divided. Muscles, the nerves to which have been completely divided, show the electrical reactions of normal muscles for some thirty-six hours after the division of the nerve. It is not until thirty-six hours are passed that the degeneration of the structure of the cut nerve has proceeded so far that it ceases to be a conductor of faradic stimuli. After section of the lower neurons—both motor and sensory—degeneration of the peripheral portions of the neurons is inevitable, since it is from the parent cells in the spinal cord or the posterior root ganglion that the neuraxon has its life. Nor can function be restored until degeneration is completed and regeneration in its train has taken place throughout the length of the divided nerve. Though the loss of function is immediate upon section of the lowest neurons, restoration of function can never be immediate upon junction of the divided ends. Nerves are not like electric wires. They must degenerate, they must regenerate, after section; and since, in our limbs, the lowest neuraxons are of

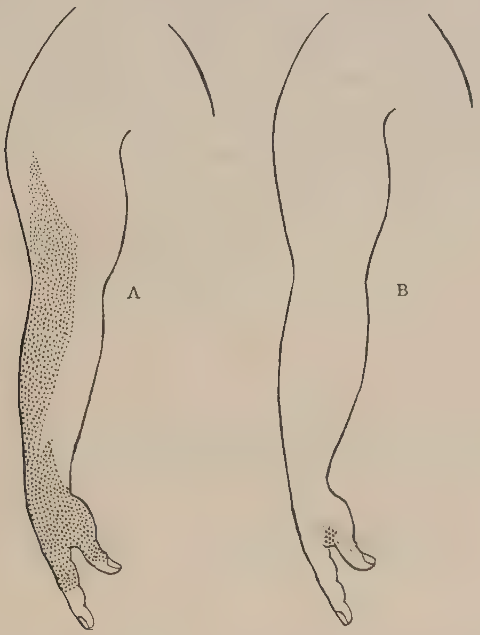


Figure 67.—(A) the area of the skin of the arm to which the musculo-spiral nerve is distributed. (B) the area rendered anaesthetic after the nerve is divided.

considerable length a period of from three months to a year must inevitably elapse before even partial restoration of function can occur.

When a lower motor neuron is divided, in such a circumstance as in cutting a nerve of a limb, there is often displayed an extremely trivial loss of the power of movement. The same trivial loss of function is often present in cases of the section of a sensory nerve, but for a very different reason. When lowest sensory neuraxons in a sensory nerve are cut, sensation is lost only over that area supplied solely by the fibres of the nerve; it is not lost over the whole area to which fibres of the nerve run. There is a vast overlap in the areas supplied by the different sensory nerves, so that the territory supplied solely by any individual nerve may be extremely small or even may not exist. It is therefore possible to cut a sensory nerve, the fibres of which run to a very large area of skin, and yet produce no area in which sensation is entirely lost (see Figure 67).

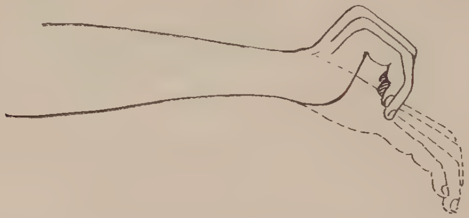


Figure 68.—Flexion of the fingers produced by extension of the wrist by a patient, all of whose wrist and finger flexors were paralysed. (From a photograph.)

If we cut a motor nerve, however, we must remember that we paralyse muscles, and that these muscles will be inevitably paralysed by the deprivation of their lower motor neuron. But the cortex does not know of muscles, it knows only of movements. We must not, therefore, think that in asking a patient to perform a movement we are asking him to use a muscle. If the patient wishes to perform a movement normally carried out by the muscles paralysed by the injury, the movement will be performed, despite the paralysis, if there be any agent that can be called upon to undertake the task (see Figure 68). This is a triumph of the pallium that, in its aloofness from details, it can compel any non-paralysed muscle that can by any trick or device accomplish the movement to undertake it and obey the volition. Very strange are the ways in which the paralysis of muscles may be ignored by the cortex and movements performed by substituted agents. No man who has his deltoid muscle paralysed may raise his arm with his platysma, but if he is a willing fellow he will surely try it. In all this there is an apparent paradox, for though it is possible to cut both motor and sensory nerves and produce a surprisingly small area of anaesthesia and an astonishingly slight loss of movement—and this by virtue of the rôle of the pallium: yet there is no skin so deeply anaesthetic and no muscles so profoundly paralysed as those whose condition is brought about by the pallium, by hysteria, or by imagination—call it which you will. A real and an irreparable injury may produce but little loss of sensation or of movement: an imaginary one may produce the profoundest degree of both.

CHAPTER XXXVII

THE CONTROL OF THE VISCERA

So far we have seen, in the development and ordering of the central nervous system, the workings of a definite process whereby all functions of the body have become increasingly integrated into an ordered whole and this entity has steadily been brought more and more under the control of that great unifying mechanism the pallium. We have seen the pallium first reinforce and then dominate other, hitherto, independent executives: we have seen it, little by little, usurp the functions of other nervous mechanisms and so pave the way for an absolute rule over the whole of the body. So far as I, as an individual, am concerned, this process has led to that which I know as I being responsible for a very great deal that my body does. But hand in hand with this process there is another that is at work in the making of the central nervous system. We have elaborated a pallium which is to concern itself with all those higher discriminative and aesthetic functions that make up the sum of human intellectual life. Are we going to permit this mechanism to pause in its consideration of the beauties of relativity or in initiating the performance of some highly skilled movement and turn aside to regulate the beating of the heart? The heart must continue to beat even if the pallium may be profoundly occupied by the contemplation of relativity. It would seem that some mechanism which, though being an integral portion of the central nervous system, possessed a maximum of independence of the pallium, were needed to control such things as the ordering of the circulation. It is the ordering of such a mechanism that necessitates the second great process in the making of the central nervous system.

Besides those nerves which constitute the lowest sensory and motor neurons and which, from their obvious connections with the spinal cord, are termed spinal nerves, there are others whose connections are not so obvious and whose course is more intricate and irregular. Since in gross anatomy the nerves belonging to this system are more easily detected in the spaces between the ribs they were named by the older anatomists the Nervi Intercostales. It was Jacques Benignus Winslow (1669–1760) who, noting their widespread communications with other nerves, gave them the modern name of *Sympathetic nerves*. Later workers appreciating the fact that the old nervi intercostales did not constitute the whole of this visceral nervous mechanism, sought for a terminology that should embrace the entire system and to-day the term *Autonomic nervous system*, introduced by Langley, is usually employed.

The autonomic nervous system is essentially a portion of the central nervous system whose function it is to regulate the visceral movements without the intervention of the higher centres. It is a portion of the central nervous system that has obtained independence of action: it is free from the overlordship of the pallium and so may perform its vital task undisturbed and it has left the pallium free to carry out its own more deliberative and intellectual rôle unhampered by the care of regulating the rhythmical movements of the viscera which are essential to life. Not only has it achieved this functional independence but it has, in the process, attained a certain degree of structural independence; and in the proper understanding of this gaining of structural independence lies the clue to unravelling the true meaning of the autonomic system.

Changes in animal structure rarely happen as isolated events; one change usually begets another, either as a necessity or as opportunity is by chance provided for the development of further modifications. It was the liberated hand that produced the shortening of the muzzle and the shortening of the muzzle that brought the eyes to the front of the face and permitted binocular stereoscopic vision with all its pallial possibilities. In the case of the sympathetic system it was the development of the coelom, which, by providing an empty cavity within the body of the animal, permitted the development of a pulsatile vascular system. In the coelenterate animal there is no space in the body in which a heart is free to contract and expand; when the coelom is developed, such a space is provided and a central pulsatile heart may drive the fluids through the tissue spaces in an ordered manner. It is in the coelomates, and only when the coelom has attained to a definite degree of perfection, that a rhythmically pulsatile heart and an ordered circulatory system are first developed. Heart muscle, and indeed probably all muscle primarily, is capable of contracting independently of the receipt of nervous impulses: nevertheless, nervous impulses are essential for the regulating of the actions of all muscles. Hand in hand with the development of a pulsatile heart there is produced a change in the central nervous system whereby some portions of it migrate from the central nervous axis and wander towards the heart and vessels, furnishing them with the nerve supply necessary for the regulation of their movements. These portions of the central nervous system, which wander away and thus gain partial structural and functional independence, are peculiar, for the migrating nerve cells are deeply yellow in colour—they are nerve cells but at the same time they are chromaffin cells. As the circulatory system becomes perfected in the phylogenetic series these primitive *chromaffin-nerve* cells differentiate and, in higher forms, the functions that were combined in the original single migrating cells are represented in two separate specialized cells—the nerve cell and the chromaffin cell. It is the story over again of the musculo-epithelial cell, the parent of the motor and the sensory cells of the more elaborated animal types. Of the primitive chromaffin-nerve cells of the lowest coelomates, the chromaffin element becomes, in the higher forms, specialized in those cells of the so-called ductless glands which constitute the *adrenal system* and the nervous element develops into the ganglion cells and the neuraxons of the *sympathetic system*.

It would seem that these early phases of the development of this system might provide clues for forming some generalized understanding of the meaning of the whole process.

With this system it is not the neuraxons that proceed from the cells of the central nervous system to bring it into relation with distal parts, but the nerve cells themselves migrate from the central nervous system towards the parts they are to innervate. Herein lies the basis of the independence of the whole system and its ability to bring about generalized and widespread action in the parts that it supplies. The initiating mechanism has wandered; it has, so to speak, left the council chamber and gone in among the crowd. In the fact that, in its inception, its nature is dual and that the adrenal system and the sympathetic system are brothers, it may legitimately be inferred that its function and that of the adrenal are originally bound together and always intimately associated. Since the action of adrenalin is well known and is dominantly connected with the vascular system, we may infer that the action of the sympathetic is mainly directed toward innervating the same system and that the development of a coelom, a pulsatile heart, an adrenal system and a sympathetic system are all co-ordinated and interdependent factors in their phylogenetic story.

In man, as in all the higher vertebrates, the wandering nerve cells have taken up their stations in various parts of the body. They compose ganglionic masses strung as beads on a string along the sympathetic chain: they have wandered into aggregated ganglia, the parents of the great visceral *plexuses*; and they have proceeded so far from the central nervous system as to mass themselves upon the walls and in the tissues of the viscera themselves. Nevertheless, every sympathetic nerve cell that has wandered from the central nervous system to some distant site, is still connected with its old home by a nerve fibre of some kind. This nerve fibre, which connects the sympathetic ganglion cell with the central nervous axis, may be regarded as a tract of the spinal cord drawn out from the cord as the cell wandered from its parent site. These nerve fibres or connectors are known as *pre-ganglionic fibres* or white rami communicantes (see Figure 69). They leave the spinal cord by way of the roots (mainly by the anterior root) of the spinal nerves and then, divorcing themselves from the spinal nerves, travel for varying distances to reach a sympathetic ganglion where they come into synaptic communication with the nerve cells of the ganglion. Pre-ganglionic fibres are of small bore, smaller than the typical spinal nerves, and for the most part they are clothed with that protective sheath, known as the medullary or myelin sheath, which is present

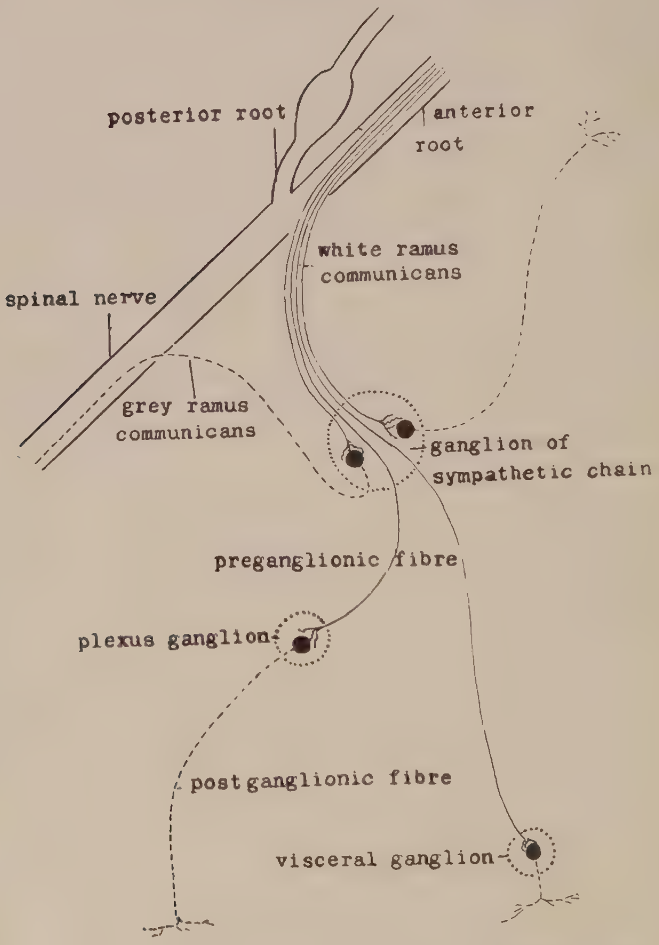

posterior root
anterior root
white ramus communicans
spinal nerve
grey ramus communicans
ganglion of sympathetic chain
preganglionic fibre
plexus ganglion
postganglionic fibre
visceral ganglion

Figure 69.—Diagram of the constitution of the sympathetic system.

in all the typical somatic spinal nerves and which gives them the white colour that justifies the name white rami communicantes. These pre-ganglionic fibres may be ranked as the upper neuron of the autonomic system. Their course within the spinal cord, before they leave it to run to the ganglia, is not so well known as are the tracts connected with the somatic spinal sensory and motor nerves. They have been traced to nerve cells in the grey matter of the lateral horn of the cord by practically all investigators. In addition, Gaskell, Onuf and Collins have traced them to the dorsal nuclear cells of Clarke's column, and Scaffidi and Biede have also observed them ending in cells of the anterior columns.

Pre-ganglionic fibres of the sympathetic system do not leave the spinal cord by way of all the issuing spinal nerves. The outflow of sympathetic pre-ganglionic nerves does not take place uniformly throughout the length of the cord: it is concentrated in relatively few segments. All those pre-ganglionic fibres that form the great sympathetic chain, which stretches the whole length of the vertebral column, are derived from the limited area of the cord comprised between the first or second thoracic and the first or second lumbar spinal nerve roots. Only the nerves issuing over this interval of the spinal cord, therefore, give off from their roots the leash of fine medullated fibres constituting the anatomical white rami communicantes. It is to be noted that the interval over which the sympathetic outflow issues from the spinal cord corresponds with the interval from which there is no spinal outflow to the limbs: it might almost be suggested that those portions of the cord occupied with the providing of somatic nerves to the great limb plexuses were too much occupied with the business to afford an additional supply of visceral nerves.

But the sympathetic outflow proper, the old nervi intercostales, does not constitute the whole of the autonomic system. There is in addition to the thoracico-lumbar outflow of pre-ganglionic fibres an outflow of similar fibres from the roots of certain cranial and lower sacral nerves. The fibres from these sources do not join the great ganglionated chain of the sympathetic, but pass as pre-ganglionic fibres to distal ganglion cells in relation to the cranial and pelvic viscera. In its anatomical arrangement this cranial and pelvic outflow is similar to the thoracico-lumbar outflow of the sympathetic proper; but, since its action upon such viscera as it supplies in conjunction with the thoracico-lumbar system is in antagonism to that system, it has received the distinguishing name of the *para-sympathetic system.*

Now it matters not if we are dealing with the sympathetic or the para-sympathetic section of the autonomic system—the underlying anatomical arrangement is always the same. There is an upper neuron consisting in a cell in the grey matter of the lateral horn of the spinal cord and a long neuraxon which leaves the spinal cord and, passing along the roots of a somatic nerve, runs in its company for a short but variable distance. This upper neuraxon then leaves the somatic nerve as a pre-ganglionic autonomic fibre or white ramus communicans. When it has left the company of the somatic nerve it travels independently for a varying distance and then comes to an end by a communication with a ganglion cell of the autonomic system. This multipolar ganglion cell is the parent of the lower autonomic neuron, and it is typical of these *post-ganglionic fibres* that they are devoid of the medullary or myelin sheath. It is for this reason that the post-ganglionic or effector fibres are typically grey in colour and are semi-transparent: this appearance having earned for them the name of grey rami communicantes. The post-ganglionic fibres are distributed in various ways. Some of them pass to the blood-vessels and by them are carried to most of the deeper viscera of the body; some pass back to the spinal nerves as the grey rami communicantes and are distributed by the spinal nerves, mainly to the more superficial parts; some pass direct to glands, or vessels, or involuntary visceral muscles which they innervate. It is to be noted that although the pre-ganglionic fibres issue only over certain segments of the spinal cord and, therefore, do not accompany all somatic nerves, the post-ganglionic fibres pass to every nerve of the body and, therefore, those somatic nerves which arise in regions where there is no autonomic outflow, nevertheless obtain their autonomic constituent by virtue of the universal distribution of post-ganglionic fibres. Two rules hold good in all cases of autonomic distribution. All autonomic impulses pass through two, and only two, autonomic neurons: every post-ganglionic fibre runs direct to the viscus from its parent ganglion. No pre-ganglionic fibre passes direct to the viscus; it always synapses about a ganglion cell, the new neuraxon from which supplies the viscus. There is an apparent exception to this last rule in the case of the autonomic innervation of the suprarenal gland, for the adrenal autonomics are pre-ganglionic. But, as we have seen, the adrenal chromaffin cells and the autonomic nerve cells are the twin offspring of one parent, and therefore in their position in the autonomic system the cells of the medulla of the suprarenal gland rank as ganglion cells.

As for the functions of this great autonomic system we have already detailed the great underlying factors. It is the system for regulating the activities of the visceral portions of the body, primarily of the pulsatile vascular system, without the intervention of consciousness and in the absence of all higher control. It is the system which, without conscious effort, controls the action of viscera and, more than that, mobilizes the visceral parts of the body for the subsequent action of the higher centres. The sympathetic proper has been termed "the mechanism of self defence," for the whole of those visceral portions of the body as have their regulation carried on in a truly involuntary fashion. The activities of the sympathetic are initially and always mainly upon the vascular system, and they are always effected in conjunction with the secretion of the adrenal glands. Stimulation of the sympathetic system causes the heart to beat faster; it brings about constriction of the lumen of the vessels and so raises blood pressure. It determines the flow of blood to the muscles, the lungs, and to the brain instead of to the vessels of the alimentary canal. It prepares the body for action and puts it on the defensive. It is the reaction to the impulse of fear; it causes the hair to stand on end, it produces the secretion of sweat, it causes "goose skin" and dilates the pupil of the eye. It contracts the sphincters of the hollow viscera and permits their muscular walls to adapt themselves to their retained contents. The para-sympathetic, on the other hand, antagonizes the action of the sympathetic in all cases in which the viscera obtain a nerve supply from both sources. The para-sympathetic slows the heart, dilates the vessels and causes a fall of blood pressure. It constricts the pupil of the eye; it activates the walls of the hollow viscera and relaxes the sphincters, thus leading to an expulsion of their contents. Between these two sections of the great autonomic system there is thus effected a complete control of the visceral functions of the body: a control that is effected without the intervention of any higher nervous centres. Nevertheless we all know that, though the autonomic system may be said to have phylogenetically and ontogenetically crept away from the central nervous axis that it might fulfil its rôle in complete independence, it has not wholly escaped the dominion of the pallium. A man by taking thought may alter the rhythm of his heart beat, and many, who in common usage are termed hysterical, can accomplish even more than this in the way of producing curious visceral manifestations.

CHAPTER XXXVIII

SOUND AND THE BRAIN

When we hear a sound the sensation that affects us is the result of air-borne sound waves which bombard our auditory sense organs. Air-borne waves may be of very different qualities. They may vary in their frequency. Air-borne waves of all degrees of frequency do not produce the sensation of sound when they bombard human ears. Of the waves that produce the sensation of sound to us, and which are sufficiently open to average human appreciation as to be available in the production of music, the variation in frequency is from about 40 a second to 4,700 a second or seven octaves. Waves of slightly lower frequency and of slightly higher frequency are capable of being appreciated, but the seven octaves represent the average human perception of air-borne sound waves capable of being interpreted as a musical note.

That the waves of lower frequency and higher frequency are not appreciated by us is a defect of our auditory sense organ. We are deaf to the very slow and to the very rapid waves because the mechanism of our ears cannot react to these waves and send their stimuli on to our brain for interpretation.

We live in a world in which we are permitted to hear only a certain range of sound; the message of the very deep and the very high is not for our ears—such waves mean silence instead of sound to man.

But all men are not alike in these things. There are many people who believe bats to be silent animals, for they cannot hear the shrill notes which fill the evening air when bats are abroad and vocal. Nor are all animals alike in this regard; the waves which mean silence to us mean sound to many creatures. I cannot hear all the sounds my cat can appreciate, not because they are too distant or too faint, but because they are beyond my range of frequency perception: they are waves of silence for me but waves of sound for my cat. And here is food for reflection. We live in a world in which waves inaudible to us are appreciated as sounds by other creatures. We cannot know the sound world of the lower animals. When all is silent to me, some other animal is listening to sounds that have a meaning for him, and more than that he is, likely enough, producing them himself. Were we to accept the verdict of many of our fellows we would proclaim the bat as a silent animal and one incapable of producing vocal sounds. But many of us can hear his voice as a distinct, loud and modulated call. What of the animals that all men deem silent and voiceless? It is likely the world is filled with animal sounds when all is silent to our ears. Someone has said that could oysters express their feelings by vocalization, our restaurants would resound with cries so dreadful that oysters would cease to appear on the menu. Short of that horrid state of affairs being realized, it is well to bear in mind that when we say that an animal produces no vocal sound we mean that it produces no air-borne waves capable of affecting our auditory sense organs.

Such air-borne waves as are capable of being appreciated by us affect in some way or other, which fortunately does not concern us here, the mechanism that is stored in the cochlea; from here they pass along the cochlear nerve and so to the auditory nervous centres in the brain. In the cochlea itself there is a collection of nerve cells, constituting the so-called spiral ganglion, and from these nerve cells neuraxons pass to the brain and constitute the cochlear nerve which, after a devious course to other ganglia in the brain stem, passes to certain nerve cell masses known as the *inferior corpora quadrigemina* and the *corpora geniculata interna* (see Figure 70). These nerve cell stations need not greatly concern us. It is enough for our present purpose to realize that, in an animal that has no auditory pallium, the essential auditory sense organ (contained in the cochlea), the spiral ganglion, the cochlear nerve with its ganglia, and the inferior corpora quadrigemina and internal geniculate bodies constitute an entity. This entity is the essential mechanism for what we can only term hearing—

hearing as deaf adders hear, as frogs hear, hearing as animals that are affected only by the biologically relevant stimulus hear—hearing, when hearing does not gain pallial representation, when its connotation is not realized, correlated, stored or associated.

In all animals in which there is a pallial rerepresentation of auditory stimuli there is a further entity, consisting of a new series of nerve processes passing from the basal nerve cell masses to the cells of the auditory cortex.

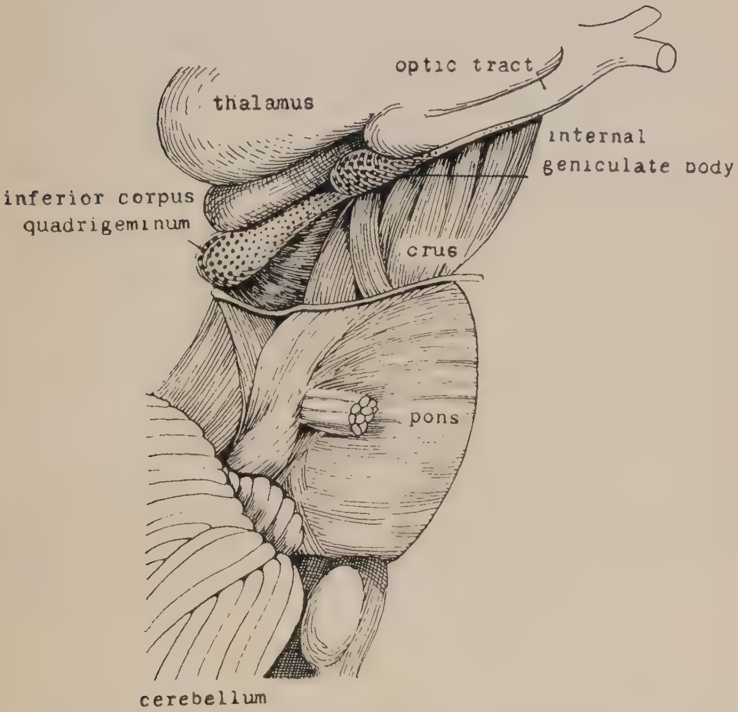


FIGURE 70.—The surface form of the human brain stem. The parts connected with hearing are marked with dots.

The nerve processes passing upwards from the basal auditory ganglia constitute the auditory radiation, and this auditory radiation ends in that pallial area distinguished by its cell structure, and limited by a sulcus of the cortex, which is known as the first temporal gyrus. We already know the difference that this new entity produces in animal behaviour: it converts the animal which was only affected by biologically relevant auditory stimuli into one capable of realizing all the auditory impressions that are capable of being appreciated by its auditory sense organ. In the animal with the neurobiotaxically grouped basal ganglia the failure to appreciate all sounds is due to its lack of auditory pallium; in the animal with the auditory pallium the limitations are only such as are imposed by the imperfections of its auditory sense organs: every sound capable of affecting its sense organ is a potential candidate for being heard. But even with pallial hearing there are degrees of perfection. All animals with auditory pallial areas cannot hear in the way so familiar to us. A frog responds to the sound of a splash because that is a biologically relevant stimulus and needs no cortex for its interpretation. But even when the auditory pallium first develops it concerns itself only with the more elemental qualities of sound stimuli; the refinements are added later. A lowly mammal must be equipped to appreciate, to associate, and to remember the noise of the snapping of a twig before it learns the connotations of the tones of a violin. It is probable that we habitually overestimate the ability of even the most familiar animals to hear in a discriminative manner. There is a difference between noise and tone, and it would seem that noise, as such, was the most potent stimulus in the case of most mammals. A rat can hear a noise, of that there is no doubt, but that it hears it in all its discriminative qualities is unlikely. Apparently a rat is entirely deaf to the musical tone of a tuning-fork: and a musical tone and silence are for the rat the same thing. With dogs the evidence is more contradictory, but in those experiments carried out with the greatest precautions against the animal receiving aids from other sources, there has never been any evidence whatever to show that tones were heard. Noise as such can be heard by all mammals, but for the most part they are completely deaf to tones.

We can learn of these things in another way: we may study human beings who are normal and those in whom some condition of disease or injury has affected the pallial auditory area. We know of deaf people—we meet them every day—people who are deaf because something has gone wrong with the auditory sense organ, or some other part of the mechanism of the ear. But we may not all appreciate from the study of normal people how far the recognition of sound is a function of the pallium, a property of the organ of consciousness.

Since man depends upon his pallium so thoroughly, we have passed into a stage in which we have almost come to rely upon the pallium to the exclusion of the basal sensory auditory ganglia. That statement may be made more clear if we say that we tend to be unable to hear unless we listen. We tend to need the cortex and to demand its intervention if we are properly to receive auditory stimuli. Take an example. The clock is ticking away upon the mantel-shelf. It may have a very loud tick. The question arises—Has the clock stopped? Can you hear it tick? Now in order to hear your own clock tick you will probably have to enjoin silence upon others and listen attentively—slowly the tick will become audible. The clock may chime and have a particularly distinctive chime. The question arises:—Is it chiming correctly? In order to be certain of this, one must watch the clock and listen for the chime when the hands indicate that the chime is due. Even then the chime may be missed in a temporary inattention. Everyone has had this experience. Everyone has missed his own clock striking. Everyone is deaf to the ticking of his own familiar clock—but a stranger coming into the room may at once note how loud is its tick or how musical its chime. This is pallial deafness, due to the fact that we have trusted to that part of the brain in which consciousness has its place and which needs attention for its proper working. From such trivial manifestations of pallial deafness there are easy grades to various conditions of, what may be termed, domestic deafness. We become deaf to the ticking of our familiar clock. In the same way children hear their parents' voices, often in admonition, so frequently that in the long run the parental voice becomes as the ticking of the familiar clock. Children often fail to hear their parents' voices, since they are so used to them, they are so accustomed to their trivial import, that the admonition is often not heeded. An extra "Don't do that" is like a tick of the clock, so familiar that it fails to arouse attention, it is not listened to, it is not heard. Domestic deafness goes further than this; it may lead to the consulting-room of the specialist. Husbands and wives from long association become so familiar with each others' voices, that their voices become as the ticking of a clock to each other. Just as the child will say, "I beg your pardon" if properly brought up, or "What?" in any other event, when its parent speaks, but hears and answers a stranger with alertness: so will husband and wife "What?" each other to exasperation. At breakfast the husband makes a comment on the bacon or the weather. The wife says "What?" The husband repeats the information in a voice that is domestically offensive. He is reproved; his only defence is that he wishes she would not say "What?" to everything he says. He is told that it is his fault for mumbling when he knows she is deaf. Here he makes a tactical mistake—he says: "If you are as deaf as all that why do you not see a doctor?" She sees one. He tests her auditory appreciation in all recognized and orthodox ways, and tells her that her hearing is perfect. Domestic deafness often costs a specialist's fee to the happily wedded: for the more happily they are wedded the more likely is the occurrence of domestic deafness. There are some people to whom no person could become domestically deaf.

In domestic deafness, in the deafness which results from not listening, there is no damage, disease, or alteration of the pallial auditory area: but from domestic deafness we may pass by easy stages to all degrees of pathological alteration of the pallial auditory area.

CHAPTER XXXIX

AUDITORY ASSOCIATIONS

In all things in which the pallium and its functions are concerned we must bear in mind that among the latest acquirements of human cerebration are those myriad psychical attributes associated with the human achievement of language as a medium for the communication of thought. We hear all sorts of sounds and among those which many of us hear most frequently are the voices of our fellow men communicating their ideas in the form of spoken words.

We have seen that through lack of attention, for want of listening, we may become cortically deaf to spoken words as we may become cortically deaf to other sounds. When we are cortically deaf from lack of listening, we do not hear the words, just as a frog fails to hear a note struck upon a tuning-fork. But with an upset in the functions of the pallial auditory area we may witness a more remarkable condition than this, for it happens that the spoken word may be well and accurately heard and yet its connotation may be absolutely lacking. In such a case the patient will say, "I hear you speaking, but I cannot understand what you say." Other sounds are heard, realized, and understood. A dog barks and the patient knows that it is a dog barking: a bell rings and the patient knows what bell it is and that it announces the hour for dinner. Only the sound of spoken words fails to be realized: the auditory appreciation to language is completely lost. The patient cannot appreciate the connotation of the simplest question put to him in words, but should his interrogator sneeze, or cough, or make some other sound, the whole connotation of that auditory stimulus will be readily realized. More than this, we partly control our own utterances by the instantaneous auditory appreciation of the words as we utter them. When the physical connotation of the spoken word is lost, the patient is in the same relation to his own utterances as he is to those of others. Though all the mechanism for framing speech may be intact, so that the patient, if he be an orator, may be mentally capable of producing a masterpiece of rhetoric, he is still incapable of controlling his speech by auditory impressions or of gathering the psychic connotation of the words he frames. Or another manifestation of upset in the pallial auditory functions may be manifested. We differ widely in our appreciation of musical sounds. To some people music is a world of romance, a world of memories, associations, emotions and delights. To others, though they realize that the ordering of sounds to which they listen is musical, and not mere jumbled noise, the whole thing means little in any aesthetic sense. But it is possible for the pallial area to fail in its functions so that all sounds however harmonious are merely heard as noise.

Another and a more profound condition of disturbance of the pallial auditory area tells us even more:—a patient may be deprived altogether of the ability to determine the connotation of any sound. It is not that words are heard but not understood, or that musical perception is lost, but no sound is understood. A dog barks, or a violin is played, and the individual is unaware of the connotation of either sound; he does not appreciate the bark as being the sound made by a dog or the music as being produced by a violin.

Here is a profound disturbance of mentality: all sounds are meaningless, though heard. One great source of information is cut off completely, not because the sense organ is deficient, but because the pallium fails in its function towards that particular sense. The sound world is meaningless; it ceases to instruct, though stimuli are carried inwards from the auditory sense organ and can produce reflexes.

In such a case we learn how great a thing for function is the whole auditory association area of the pallium: we realize somewhat what is the life of a lower animal that possesses no pallium to which auditory impressions find their way. And indeed we know this from our own normal experience of ourselves and from the observation of others.

Think of the complex associations which come irresistibly to the mind when some sound is heard. Whole scenes, whole complexes, imperatively following in the wake of the receipt of, perhaps, a not very remarkable sound. The siren of a liner sounding through the fog, the "all clear" after an air raid; the whizz of a flying shell; for some, these—even faintly caught—mean vast complex association pictures, emotional states reacted, and whole pages of life into which sensations of all sorts come huddled, resistless, and overwhelming. Or it may be some more subtle note—the throb of a harp string, the call of a bird, or a snatch of music: everyone can live through whole scenes in which every sense is involved when, by chance, some such faint sound is caught.

For some, sounds mean even more than this. Sounds may do more than merely recall associations: they may conjure up other sensory impressions which have never been associated with them in experience. We have all been told that to blind men, sounds at times provide a substitute for colours. There are many grown-up people —and many more children—to whom sounds, especially the sounds of words, carry not only the connotation usually ascribed to them but also produce an impression of colours. To those who do not possess coloured words this thing is meaningless in whatever way the subject may be presented to them. Nevertheless, we must admit that the sound of a word may, in some people, call up an association that involves more than that which is ordinarily understood to be the connotation of the word, for it may irresistibly bring into the sphere of consciousness the realization of a colour. Take, for example, the spoken word "Wednesday": for each of us this will have associations. Wednesday may be a day we dislike or like by reason of some routine task or some accustomed relaxation. Wednesday is a definite day of the week and as such has associations, suggestions, and memories. But, for some, the sound of the word Wednesday may imperatively produce an impression of rich deep yellow. Here is a complexity in the functions of the human pallium:—and the sound-colour combinations of many go far beyond the innate associations of yellowness and Wednesday.

Apart from representations in the association areas of the auditory pallium, think of the sound memories. We have all met people who could remember in an astonishing manner things they have once heard. Some men may go to a musical comedy and be able to reproduce a great part of the whole of the auditory nonsense with the greatest precision and minuteness of detail. Some will not remember a single tune, or the words of a song, or any of the patter which epitomizes musical comedy cleverness—but will recall, maybe years afterwards, scenes, dresses and peculiar or comic actions, or expressions, which went to the making of the thing. Some men will remember whole passages of a recited poem, of a sermon or a lecture; some will recall only the scenes, and dwell on the gestures and the appearance of the orator, having no more than a general impression of the poem, the sermon or the address. Some, when introduced to a stranger, will remember for ever that they have met Mr. Soandso, some only that they were introduced to a gentleman with a Roman nose and heavy eyebrows, whose face and method of smoking a cigar they will never forget. Some people have auditory sensations as a predominant memory sense. To these a spoken message may be safely confided; they will remember it in every detail without mumbling it to themselves at intervals as others must.

Now in all this there is a worldly everyday interest. The man who has predominant auditory memories and associations has his usefulness and also has his limitations. If he finds himself in a sphere in which auditory memories and associations lead to success, he will be considered a capable man; but he would be a failure were his task to consist in recognizing individual differences in a series of objects: he would make a poor systematic zoologist, a poor artist, a hopeless bushman, though he might be great in many other, and more important, walks of life. It may be that this thing is not always fully recognized by those whose duty it is to teach others. There are some who learn, remember and associate by auditory channels: and many who rely upon other senses. For those who learn by auditory channels, the lecture, the spoken word, the oft-repeated simile, the mnemonic are all important. There are scholars whose whole education is obtained in lectures and whose entire mental storehouse consists in remembered passages, in memories of discourses or even in that debased form of auditory memory comprised in jingle rhymes. There are others who are happily anaesthetic to the lecture and the mnemonic device, but who remember the things written on the blackboard or the diagrams used to illustrate the lecture. He is the fortunate teacher who can cater for both classes: but of this I am assured, that no student whose auditory associations and auditory memories are dominant, though he may excel in other academic subjects, will ever excel in the study of anatomy. Every teacher should remember this: in his class there will be some who learn and associate by auditory impressions and to them his lecture may be useful; but there will be many who learn by other channels and for these he must also cater if he is to teach successfully.

Now although our pallial area for auditory impressions, memories and associations is a wonderful thing, we have seen that, compared with some animals, our auditory appreciation, as it is dependent on our sense organs, is comparatively low. We cannot hear all the sounds that some of the lower animals can appreciate. Again, we probably do not have so accurate a spatial appreciation of sound as do many lower animals. We have only to watch an animal that relies largely on hearing as a guiding sense; we see its mobile ears constantly on the move, cocking this way and that so that the direction of sounds may be accurately localized. Such an animal has a far more complicated external ear or pinna than that possessed by man, and this highly developed, highly functional pinna certainly gives its possessor far more information as to the spatial relations of sound than is available to us. In most animals in which auditory perception is very acute there is also an anatomical mechanism of the ear which we do not possess. Many animals can fold their ears during sleep, and in these animals the tube by which sounds are conducted to the auditory sense organ is closed by the fitting of the sculpturing of the folded pinna (see Figure 71). We have seen that eyelids are needed to shield the brain from the bombardment of visual impressions: there is a sound life for many lower animals so imperative that closure of the ears is necessary if the pallium is to have rest. Our auditory sense organs are as much open to the receipt of auditory stimuli when we are asleep as when we are awake. But when we are asleep our pallium has not its waking attention for auditory impressions. Just as with sensation and movement, auditory appreciation may be lowered by cortical inactivity; domestic deafness is a normal manifestation of what, when more seriously developed, is known as functional, hysterical, or cortical deafness. So also, just as a heightened awareness of the body may be the outcome of heightened cortical activity, an unduly acute appreciation of sound may be a manifestation of auditory cortical hyperactivity. There are days for all of us when sounds are more vividly heard, days when we are more irritated by the noise of banging doors, or of conversation or the sounds of the neighbour's gramophone—days when sounds bombard the pallium more than is their wont. So too may this hyperacusis become pathological and just

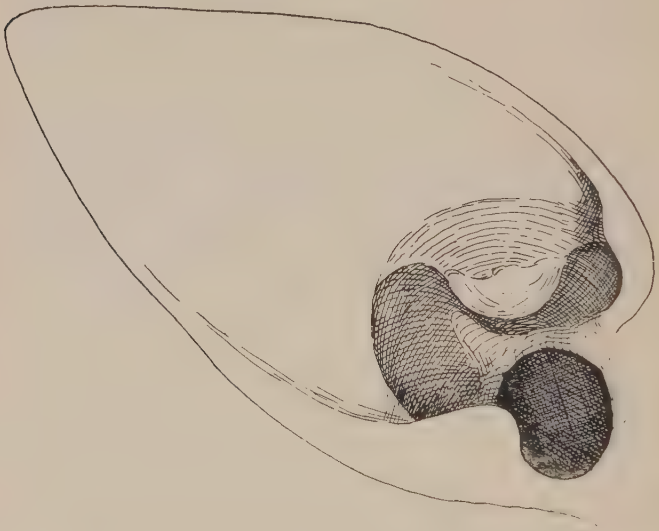


FIGURE 71.—The complicated external ear of a lower mammal. The ear figured is that of the Australian Opossum, an animal that folds its ears during sleep.

as the pallial upsets of warfare produced cortical deafness so did they produce that strange condition whereby a patient was rendered well-nigh distraught since his hearing was ten times as acute as normal.

CHAPTER XL

THE PHOTOSTATIC SYSTEM

When we speak of the function of vision we speak of a complex, if we are dealing with vision as this phenomenon is manifested in ourselves. It is because vision in man is a complex that we have a difficulty in realizing any form of vision that in any way falls short of the complication of the sensation as it is manifested in man. Long before there was such a thing as vision, in the sense that objects were seen and pictured, there was a function of light sensitiveness. Just as scent is a guiding sense, so is light a guiding sense, and light sensitiveness is a primary element in the complex that afterwards becomes known as vision. Seeing is not the foundation of vision, it is the outcome of the development of a primitive light sense.

Scent is a guiding sense, sound is a guiding sense, and in the same way a sensitiveness to the presence of light is a guiding sense. We may say that, primitively, nothing is seen, but light and absence of light are appreciated by a definite placode or sense organ. It may be advantageous for the animal to move towards the light or away from it. In either case a definite series of connections of the receptive organs with other parts of the nervous system will be brought about by the agency of neurobiotaxis; and a definite advantageous response to the stimulus will be established. Light as a guiding sense enables the animal to adjust its own disposition with relation to this stimulus. Light or the absence of light dictates its movement and its poise. We may, therefore, speak of this primary evidence of the influence of the development of an organ capable of being influenced by the rays of light as the *photostatic element of vision.* In an animal that has a primitive sense organ capable of being influenced by light rays, the appreciation will be of light or the absence of light. There will be no vision in the sense that pictures are seen, but light as a stimulus analogous to sound or touch or scent, will be responded to. The reaction produced by the neurobiotactic grouping of the nerve centres will be an appropriate, life-saving one, and it may result in the animal turning towards the light or away from it. In man this basal photostatic element of vision is retained and anatomically it is readily identified in that portion of the optic tract that passes to the *superior corpora quadrigemina* and so to the posterior commissure and the posterior longitudinal bundle of nerve fibres (see Figure 72). The superior quadrigeminal bodies are, in man, relatively small masses—the diminished remnant of the great corpora bigemina of the lower vertebrates—and they are the neurobiotactic cell stations for the photostatic elements of vision. From these cell stations connections are established with the nuclei of origin of all

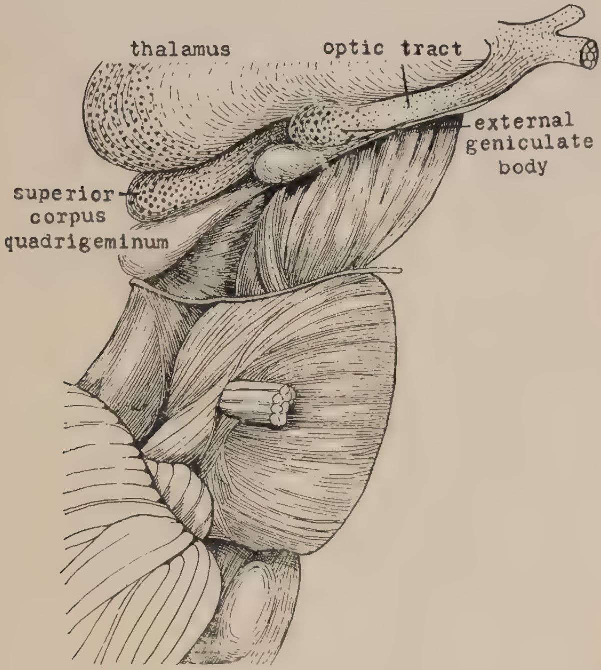


FIGURE 72.—The surface form of the human brain stem. The parts connected with vision are marked with dots.

the motor nerves that produce eye movements, with the nuclei of the motor nerves that produce movements of the head and neck, and ultimately of every part of the body. The pathway by which these connections are established is that bilateral strand of white fibres which runs downwards in the brain stem beneath the floor of the aqueduct of Sylvius and of the fourth ventricle, and which is known by the name of the posterior longitudinal bundle. By way of the posterior longitudinal bundle the photostatic impulses are brought into correlation with those derived from the spatial, static, balancing impulses derived from the labyrinthine system by the vestibular nerves, with the auditory stimuli brought by the cochlear nerve and with the controlling influence of the static regulating mechanism of the cerebellar system. It would be difficult to cite a better example of the basal neurobiotactic grouping of sensory and motor cell stations in the human brain than this system of the photostatic impulses. A minimum of attentive study will demonstrate the reality of the curious stringing together—as beads upon a thread—of the motor nuclei concerned with eye movements and body poise in relation to the instreaming stimuli produced by light (see Figure 16). The superior quadrigeminal bodies are the receptive centres for light stimuli; the posterior longitudinal bundle is the thread, and the nuclei of origin of the motor nerves of the eyes and of the head and neck are the beads which are strung upon it by the agency of neurobiotaxis.

The fibres of the optic tract which, being photostatic in function, run to the superior quadrigeminal body and so to the posterior longitudinal bundle and establish these widespread silent connections, do not have any direct path to the cortex. Though the other elements of vision passing in the human optic tract to the nuclear masses of the brain stem have relays, passing as new neuraxons to the visual area of the cortex, it would seem that the photostatic fibres, which find their cell station in the superior quadrigeminal body, do not pass to any higher level—they have no highest neuraxon passing to the cortex. That is as one would expect. The eye is exposed to light, the muscles of the pupil and those controlling the lens react, the eye is moved, the head moves in harmony, the movements may extend further afield, and yet the whole business is without our ordering. There is, to put it crudely, no voluntary mechanism in this, it is an involuntary or reflex photostatic reaction, a reaction in which light as a mere guiding sense is the underlying stimulus. We cannot restrain nor regulate the dilatation of our pupils when light is diminished. The impulses to the centre that regulates the pupillary muscles by way of the oculo-motor nerve are carried direct from the photostatic centre in the superior quadrigeminal body. We cannot restrain nor regulate similar movements when the impulses derived from loud noises affect the posterior longitudinal bundle by way of the cochlear nerve. Nor have we any control over eye movements evoked in response to stimuli streaming from the labyrinth through the channels of the static pathway of the vestibular nerve. In man there is retained as an entity the mechanism that comprises the sole visual apparatus of those animals possessing nothing but a light appreciation sense.

In man, however, this factor is so thoroughly dominated by the other elements of the complex of vision that it is but a subordinate function and one whose anatomical cell station—the superior quadrigeminal body—is relatively trivial. We have only to contrast the small superior quadrigeminal bodies of man with the vast bigeminal bodies of the lower vertebrates to realize how small, but nevertheless important, an element of vision is the basal photostatic element. Light is so much more than a guiding sense to us that it is difficult to picture the condition of those creatures of which one may say that they see somewhat as we smell. To them light, like scent, is a stimulus, it is not a thing that creates pictures, visions and dreams. It is a stimulus to be reacted to in one direction or another as the neurobiotactic grouping of the motor nuclei dictates. Though we cannot easily realize such a condition, nevertheless, we may witness it in man. If the visual area of the cortex is destroyed in man the result is blindness—the patient cannot see, but his pupil still reacts to the light stimulus—the photostatic mechanism is intact though the patient is blind.

CHAPTER XLI

THE ELEMENTS OF VISION

A lowly reptile, such as a Blind Worm, can see the slug upon which it feeds. There is no doubt of that. We may be uncertain as to what other stimuli may appeal to its visual sense; but that it can see the slug that is to be its victim, in that moment when it examines it and poises over it, is certain.

From its behaviour it is obvious that light is to it far more than a mere guiding sense:—to its primitive photostatic system it has added something more. It not only appreciates the presence or absence of light, but it sees illuminated objects. It can appreciate degrees of luminosity. It has what we are accustomed to term a sense of vision. Nevertheless, of all illuminated objects within its range of vision only a few are seen: and these are of life-saving importance. Something has been added to the functional hierarchy of vision; but many elements of vision, as vision is known to us, are still lacking. If any lower vertebrate be attentively observed, it will be noticed that of the comparatively small number of visual stimuli that produce an obvious effect upon it, those of which movement of illuminated objects is a component part are dominant. A Blind Worm, into whose range of vision a small slug creeps, becomes at once alert. It is obvious that the moving slug has produced a picture on the retina of the Blind Worm which has excited a definite and appropriate response. If the slug does not move the appeal seems to be altogether wanting; and an imitation slug does not, in my experience, produce any visual stimulus whatever.

A very perfect, but entirely immobile model of any form of living prey seems to be altogether unperceived by any lowly reptile accustomed to feeding upon living creatures. A predatory fish will dash for a moving object, an artificial fly, a spoon, a piece of red flannel—anything moving through the water. It is the movement of the illuminated object, and not so much the intrinsic nature of the object itself, that is the visual stimulus. Though the highly evolved dry-fly fisher may have other and far better theories that apply in the case of his favourites, it is nevertheless true that with many predatory fish, such as the Barracoota, a piece of a cigarette tin, or part of an old sock, are quite as effective, when used as a trolling bait, as is an actual fish or its most perfect imitation.

Snakes, as everyone connected with a zoological garden believes, must be fed on living prey; and in many instances this is quite true. Such snakes as will feed in captivity must have living, moving creatures supplied to them before they will attempt to pursue and capture and finally ingest their meals. Even if they will eat dead animals these animals must be moved about in the semblance of life before their presence is appreciated. It is true, as a generality, that snakes require living victims, but it is not true for the reason that snakes can discriminate between the living and the recently dead as a problem in dietetic values. It is true, because the living animal moves, and movement of illuminated objects is an adequate visual stimulus to a snake. Even with us, with the whole wealth of our visual perceptions, movement is a great incentive to visual appreciation. Every field naturalist is well aware of this. A pike in the shadow of a bridge, a lizard on the wall, may be entirely ignored as a visual picture until some slight movement reveals, as we say, its presence.

Every collector of mammals, birds, reptiles or insects, and every sportsman knows this very well. It is an everyday experience that the much-desired specimen is seen only when some slight movement has produced a visual stimulus all too late, and the sweep of the net or the shot is effected when the creature is beyond range. We make movements to, as we say, attract attention. But with us movement is only a comparatively trivial factor, since it is one of many, in the whole complex of visual appreciation. With some of the lower vertebrates, however, movement of illuminated objects is the most important factor that determines the existence of vision as an extension of light appreciation. How keen is this perception of even minimal degrees of movement in the case of the typical mammals is often overlooked by those who make experiment in animal behaviour, though it is properly appreciated by animal trainers. Animals educated as performers on the stage may learn to recognize and respond to movements made by their trainers that pass altogether unnoticed by human onlookers. The animal will take its cue from a possibly unconscious attitude of expectancy on the part of the trainer, made when the trick is to begin, and from the slightest movement of relaxation, expressing final satisfaction, when the trick is successfully terminated. How slight these movements may be is well demonstrated in Pfungst's investigation of the Elberfeld horses, for in this notorious instance there is little doubt but that Clever Hans, the so-called "Thinking Horse," performed his part instructed by the visual stimuli derived from the slightest, and probably unconscious, movements of Von Osten, his master. The same dependence upon visual stimuli has been shown to account for the many other cases of "thinking" horses and dogs, for the explanations of which thought processes equalling, and indeed even exceeding, those of human beings, have been claimed for the animal. In all tests of sensory perceptions carried out upon animals, this ability to appreciate and interpret minimal movements made by the investigator or his assistants must be reckoned with.

Realizing this dominant appeal of movement as a visual stimulus we may readily appreciate the value of that common phenomenon miscalled feigning death. When a creature, as we say, feigns death, it does not deliberately pretend to be dead. The term is an extremely bad one, since its use almost inevitably creates the mental postulate that the living animal is aware of the condition of death and assumes the attitudes and appearances characteristic of the condition. The insect that feigns death has no regard for the preference of its enemy for living or dead sources of nutriment. It is not pretending to be dead, but is assuming a position of complete immobility. Movement appeals as a visual stimulus to its enemy; but visual appreciation may not have extended to the stage of perfection of interpreting the details of an illuminated object that is absolutely stationary.

The so-called feigning of death is a very widespread phenomenon. It extends even to the birds and mammals if we include the instantaneous freezing into immobility displayed by such birds as *Podargus* and such mammals as *Trichosurus* and many others.

The very extension of the phenomenon so far afield is a guarantee of the very dominant importance of movement as a visual stimulus high up in the animal scale. In connection with this question it is worth while to turn aside to consider this phenomenon of death feigning from another point of view. There is a growing school of biologists which considers that such adaptations as protective mimicry and death feigning are devoid of reality. There are those who declare that "many an apparently beautiful adaptation has been shown to be non-existent" (Lotsy). There are those who boldly state that adaptations do not in fact exist. But it may be that this school has in some cases shown them to be devoid of reality when they are examined by a human eye, possessing all the complexes of human vision and linked to a human brain. A spider feigning death may be, to our vision, a creature adopting an absurd rôle, since we may detect the deception with very little experience. But we must remember that, when movement of illuminated objects is the dominant or almost the sole visual stimulus, an entirely quiescent spider—not feigning death, but remaining indefinitely still—ceases to be visible to its enemies. The reality and the success of adaptations must not be assessed by our estimate of them; they must be judged from the standpoint of creatures whose function of vision has not been elaborated to the complex perfection of this sense as it is developed in us.

What the sense of vision in the lower animals actually connotes is, of course, very difficult for us to estimate. In all questions of sensory perceptions it is difficult or impossible to take the standpoint of a creature not so completely equipped as ourselves.

There are, however, two ways in which some understanding may be arrived at. We may watch the recovery of human beings in whom damage of the visual areas of the brain has caused loss of vision or we may study the visual appreciations of lower animals by the method of conditioned reflexes.

When a human being has suffered damage to his visual cortex so that he has become cortically blind, his eyes still remain as perfect optic sense organs. Such a patient at first sees nothing, he is blind; but his photostatic element of vision remains intact, his pupils will react to light in a perfectly normal manner. As his cortical disturbance is recovered from he next obtains an appreciation of luminosity and movement. He sees, but his vision is extremely imperfect. In the early stages of recovery his vision is mostly confined to the periphery of his visual fields. At this stage, a cortically blind man, who is being led along a darkened street, will know that there is a difference when the whitened curb of the pavement is crossed. A difference in luminosity has appealed to his peripheral visual field. As he walks along in daylight he will become aware of a visual stimulus created by the movement of the feet of his fellows along the pavements; and in this stage it may be positive discomfort for a cortically blind man to travel in a corner seat in a railway carriage, since the moving landscape will create a constant visual stimulus to him. This gives us an imperfect picture of the visual perceptions of such creatures in which luminosity and movement of illuminated objects are the main effective visual stimuli. When we study lower animals by the method of conditioned reflexes we may learn more. In brief this method consists in forming an association between some sensory stimulus and the ingestion of food.

We may be accustomed to associate the auditory stimulus of the dinner gong with the taking of dinner. In an animal, such as a dog, any reflex which can be associated with the receipt of a meal will produce a flow of saliva. If one grade of sensory stimulus has become the effective stimulus by association, other grades of the stimulus will be inoperative. In this way it is, with much patient experimenting, possible to learn the grades of stimulus that the animal can appreciate. If one degree of luminosity has become the stimulus which produces the reflex, it can be determined how large or how small a departure from that degree of luminosity is differentiated and so fails to produce the reflex. In this way it is impossible to inquire into the visual stimuli that are operative in the case of the low vertebrates we have been considering; but in the case of such mammals as the dog the question has been very thoroughly explored. With the dog, the appreciation of degrees of luminosity is even more acute than it is in man; minute grades of luminosity, imperceptible by us, are differentiated by dogs. Minimal degrees of movement are likewise readily appreciated. But shape and form of objects are poorly distinguished. With the dog and with the cat and all the mammals lower than the Primates, colour if it is appreciated at all, as distinct from luminosity, is only the feeblest stimulus: and the evidence is all in favour of such creatures being accepted as colour blind.

That vision which appreciates differences of luminosity, which readily detects movements of illuminated objects, but which has a poor appreciation of form and none of colour, is a vision of light and shade and motion. It is the flat, monochromatic vision which is typical of most of the lower mammals, and is termed *scotopic vision*, since it is that form of visual sense present in crepuscular animals whose activities are passed in degrees of low illumination. The scotopic, or dark-adapted, eye is an advance upon the eye which is merely an organ for the recognition of light rays: nevertheless, compared with our eyes, it is an incomplete organ of vision. To realize scotopic vision we must imagine a monochromatic, flat picture in which outline is not very vividly marked and in which form, spatial relations, colour and the finer attributes of our vision are lacking. Such a vision occurs in human beings in recovery from injuries of the cortical visual area. The scene is as monochromatic painted scenery in a theatre, everything is flat, nothing is projected in space. The opposite side of the street may be only the distance away of the breadth of an ordinary street or it may be further away, or so much nearer that one may bump into it at the next step. An object that is small may be small because its actual size is small or it may appear small because it is far away. We are able to form a judgment on these matters for our vision takes account of spatial relations; but when recovering cortical blindness has reached the stage which is analogous to scotopic vision, the patient cannot make this judgment. This condition is well illustrated in the case of a man recovering from cortical blindness caused by an occipital injury inflicted during the European war. The patient was a country man and had never seen an elephant, and upon being shown one that was walking in the distance he expressed great indignation at what he supposed was a hoax; for elephants, as he well knew, were large animals and this thing was no bigger than a well-grown collie dog.

The typical mammalian scotopic vision appears to be largely administered by those sensitive retinal elements which, from their typical form, are known as rods in distinction to other elements known as cones. There is some reason for believing that the retinal rods are the sensory receptors that subserve the function of scotopic vision; but we must not neglect the central connections and the cortical elements that come into play in the full perfection of vision as we know it.

Scotopic vision is a stage in the development of the full sense of seeing; it is a special kind of vision with its own possibilities and its own limitations, and it has therefore been termed the *protopathic* or *dyscritic* stage of vision. Scotopic vision, the vision typified by the rod element in the retina and characteristic of lower and crepuscular mammals, is a vision that can appreciate degrees of luminosity and movement with great acuity. Despite its perfections in its own way, scotopic vision has its limits, for the animal with only scotopic visual sense sees a monochromatic world, colour free, flat, and made mostly of varying degrees of illumination and the movements of illuminated objects. There is in the central connections of the optic nerves in the lowest mammals a parallel with what we have seen in the case of sensation. We have seen that for the photostatic sense, the superior corpora quadrigemina and the external geniculate bodies are the chief central cell stations; but with true vision other centres come into play. The optic nerves run also to cells in the posterior part of the thalamus, which thereby becomes entitled to its older name of optic thalamus, and from the thalamus they are relayed to the visual cortex by the visual radiation. But, as we have seen with other functions, the cortex is at first more of a luxury than a necessity for visual appreciation. So much would be inferred from Lashley's experiments with white rats. The rats were trained to respond to light appreciation and when their education was complete their visual cortex was removed. At once they failed to perform their usual rôle dependent upon light discrimination. But though the results of their education to light stimuli were lost with the removal of the visual cortex, they could still appreciate the presence of light. More than this they could again acquire the whole of their previous repertoire; they could learn by educating their lower centres, presumably the thalamus. Here then the thalamus appears to be the great sub-pallial receptor for visual stimuli of the more crude and less discriminative sort, the pallium is the addition that makes possible the discriminative, spatial, and aesthetic elements of vision.

CHAPTER XLII

COMPLETED VISION

Many factors go towards the making of a visual sense such as we know it from our own sensory experiences. To us, vision means far more than the seeing of illuminated objects as flat monochromatic outlines whose distance from our eyes is not made apparent from any relief they may possess in the visual picture.

We can appreciate form, distance, spatial relations and the colour of objects seen: we have passed from the stage of low illumination or scotopic vision to the possession of a discriminating sense of brightly illuminated objects: such vision is termed *photopic* and by some it is recognized as the *epicritic* element of vision.

The whole complexities of photopic vision are present only in the Primates among the mammals and in the phylum of the Primates the evolution of the various stages of perfection may be traced with some degree of certainty if we have concern both for the anatomical findings and the actual observed facts of animal behaviour. That vision under conditions of a high degree of illumination is not a possession peculiar to the Primates is obvious: there are many mammals accustomed to using their eyes in the full glare of daylight. Nevertheless, the bulk of the mammals are crepuscular or nocturnal in their activities and possess dark-adapted eyes. Such animals are at a disadvantage when forced to be active in broad daylight and the apparently stupid behaviour of animals with scotopic vision when caught abroad in the glare of bright sunshine is evidence of this. This fact is not always recognized in estimating animal behaviour. Many a crepuscular or nocturnal mammal will appear stupid when its activities are watched in daylight; but it is a very different creature when illumination has become sufficiently low to permit its scotopic eyes to function properly.

It is often supposed that some animals prefer to sleep by day whilst others prefer to sleep by night. It is easy for us with our light-adapted eyes to understand why some animals sleep at night: but it is often overlooked that the animal with the thoroughly dark-adapted eye is awake at night because it is then that it can see and is asleep by day because, in bright illumination, its eyes are as little use as ours are at night. An Australian Opossum comes abroad in the dusk because then it can see most clearly, and no amount of feeding by daylight or petting by daylight can ever turn it into an animal of daylight activities.

In the warfare of animal life the dark-adapted eye and the light-adapted eye play large part.

There are diurnal birds of prey and nocturnal birds of prey, or, as we might say, birds of prey with scotopic vision and birds of prey with photopic vision. There are diurnal carnivorous mammals and nocturnal carnivorous mammals. Each hunts when the conditions of illumination are most suited to its type of vision. As for the hunted, woe betide him if he be caught abroad when the conditions of illumination are unsuitable for him.

In the arboreal stock of the Primates, daylight activities were early established. The Tarsiers are nocturnal, some of the lower monkeys are crepuscular, but the vast majority of the Haplorhini are children of the daylight.

Every circumstance of the arboreal life of the haplorhine Primates is conducive to daylight activity; the Primates wake at daybreak and retire to sleep at sunset; they are impudent in the sunlight but apprehensive in the dusk. Doubtless an Australian Opossum dreads the daylight, in which it is at a disadvantage and in which it is at the mercy of those predatory animals whose eyes are adapted to high degrees of illumination. Certainly the monkeys with light-adapted eyes are apprehensive of the dark: and we have enough of the Primate ancestry in us to give us still a dread of the dark. Cats, we say, can see in the dark. Nocturnal beasts of prey with dark-adapted eyes are our masters when daylight ceases. We are at a disadvantage when the world has ceased to be brightly illuminated and all mankind, having revelled in the aesthetic perfection of his photopic vision in the daylight, dreads the dark. To be afraid of the dark is, by the stouter amongst us, considered to be a childish weakness: it may be that it is so, but we must admit that it is an inborn heritage of a defenceless animal of arboreal ancestry and with a light-adapted eye such as we happen to be.

That the uninformed sections of humanity should dread such an event as the eclipse of the sun and make the occasion one for the display of elaborate ceremony, is only natural. It is the daylight, as opposed to the dark, that gives us and our phylum a puny supremacy over those physically better-equipped mammalian rivals that are abroad by night. If childish be synonymous with natural, then we may admit that it is childish for Man, with all his contrivances for the production of artificial light, to be afraid of the dark. We may also find a clue to his restless quest for artificial light. Light—for his light-adapted eye—is what Man is for ever seeking; for with perpetual light he will be perpetually supreme.

But in the attainment of our complete sense of vision more than mere intensity of illumination is involved. Many of the ungulates and some of the carnivores are fully as diurnal in their activities as is Man himself. Several circumstances combined to create for the diurnal Primates new possibilities of development of the power of vision. In all these circumstances the fore limb, emancipated from its office of supporting the body weight, and the hand, freed for a multiplicity of functions, played greatest part. When the hand is freed for its duties as a grasping organ, it becomes at once the elected member by which food is obtained and by which it is carried to the mouth. Some animals obtain their food by seizing it, cutting it, browsing it, or grazing it with their teeth; others, when the fore-limb is liberated, employ the hand for this office. When an animal obtains its food with its mouth, it is necessary for the muzzle to be prolonged so that the front teeth may be well in advance of the eyes. When the hand is employed for conveying food to the mouth the muzzle becomes shortened and the face becomes flat. The long-faced grazing, browsing, or nibbling animal is in marked contrast to the flat-faced monkeys. As the muzzle shrinks back and the face becomes flat, the eyes themselves come to occupy a very different position and to be directed in a very different axis. With this anatomical alteration there comes about a vast change in the visual field. When the eyes are set at the side of the head, with an elongated muzzle projecting between them, the animal possesses two *separated monocular fields of vision* (see Figure 73). The right eye sees the field on the right side of the animal and the left eye sees the left field, these two fields being separated. With progressive shortening of the face, and especially with varying degrees of prominence of the eye-ball and completeness of the bony orbit, the previously separated monocular fields meet in front and the animal then possesses *combined monocular fields of vision* (see Figure 74). It is possible that in some animals, such as hares, in which the eyes are unusually prominent, the combined monocular fields may meet both before and behind and so produce *panoramic fields* by which

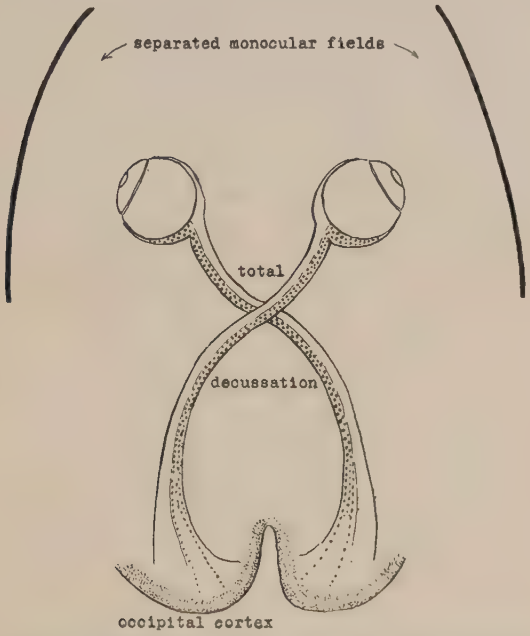


FIGURE 73.—Diagram of the eyes and optic tracts at the stage in which there are separated monocular visual fields, absence of consensual reactions of the pupils and of conjugate movements of the eyes, with total decussation of the fibres of the optic nerves.

the animal may have the whole circumference within its field of vision at the same time. The next step towards the development of the typical vision of the Primates is that shortening of the face, and consequent bringing of the eyes to the front, which causes an overlap of the two visual fields and results in the production of *binocular vision* (see Figure 75).

Binocular vision is a thing of altogether different quality from monocular vision, since the appreciation of relief and spatial relations now becomes a possibility. The final step is made when objects at near range, held in the hand for purposes of examination, are brought under the critical inspection of the eyes. The axis of the eyes becomes fixed upon the object to be inspected and the condition of a *binocular fixation field of vision* (see Figure 76) is developed.

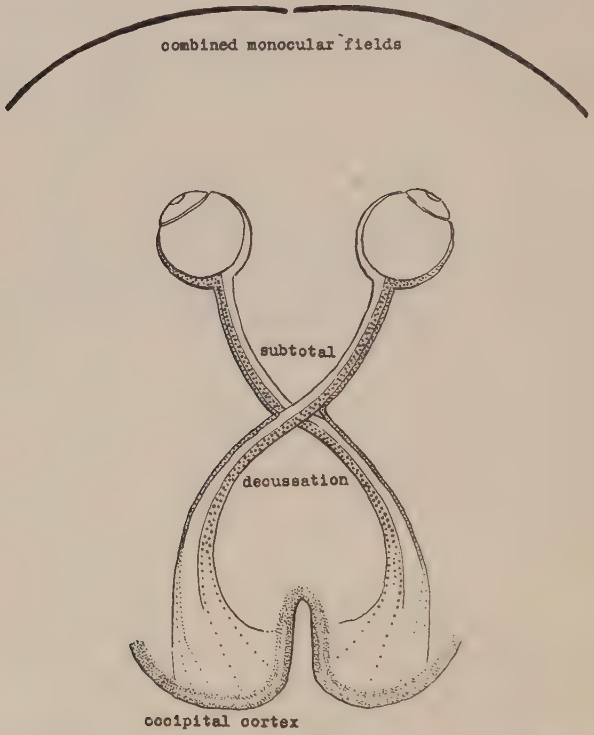


FIGURE 74.—Diagram of the eyes and optic tracts at the stage in which there are combined monocular fields, some consensual reaction of the pupils and conjugate movements of the eyes, with subtotal decussation of the fibres of the optic nerves.

Now all these things may be said to be the by-products of the evolution of parts primarily unrelated with the eyes; how do the changes affect the eyes themselves and the sense of vision that they subserve?

In those animals in which there are separated monocular visual fields each eye may be said to be a separate unit, and vision to consist of two separate, unrelated, flat monochromatic pictures. Each eye acts as an individual entity.

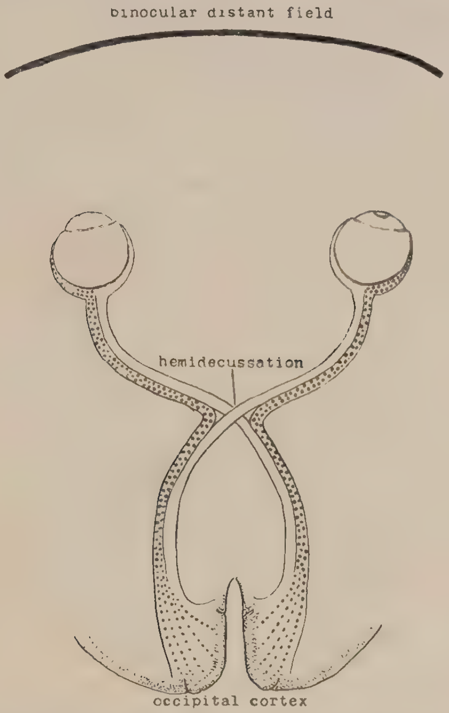


Figure 75.—Diagram of the eyes and optic tracts at the stage in which there are developed a binocular distant field, completely consensual reactions of the pupils and conjugate movements of the eyes, with hemidecussation of the fibres of the optic nerves.

The reflex reactions of the pupils are entirely separate—there is no consensual pupillary reaction—and the movements of the two eyes themselves are independent—there is no conjugate ocular movement. Absence of consensual pupillary reaction and absence of conjugate eye movements are found in many of the rodents in which there are separate monocular visual fields. In ungulates, there appears to be some slight power to produce conjugate movement of the eyes, and in the shorter-faced carnivora there are developed consensual reaction of the pupils and more complete conjugate movements of the two eyes.

Amongst the Primates, conjugate movements of the eyes seem, in Tarsius, to be largely subordinated to movements of the head; but this appears to be a mere question of economy of movement, since presumably it is a more simple matter to produce rapid movements of the head than to carry out combined movements of that animal's enormous eyes. In all the remaining monkeys there are perfect consensual action of the pupils and conjugate movements of the eyes.

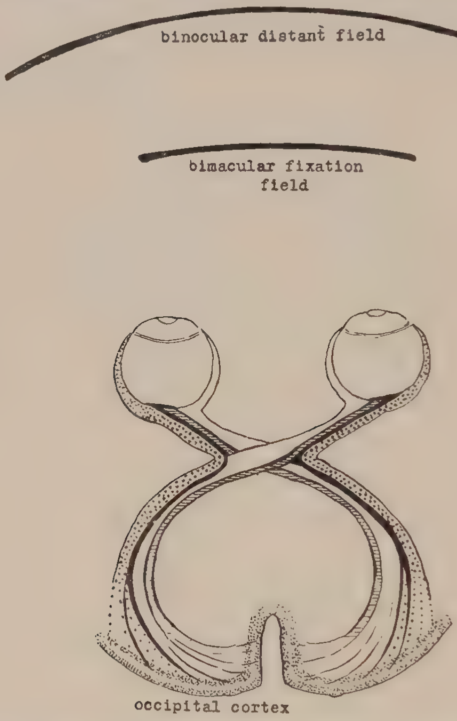


FIGURE 76.—Diagram of the eyes and optic tracts at the stage in which there are developed a binocular distant field, a bimacular fixation field, complete consensual reactions of the pupils and conjugate movements of the eyes, with hemidecussation of general retinal and macular fibres of the optic nerves.

Now, when each eye is a separate unit, performing its own independent movements, and having its own detached visual field it is connected by its optic nerve, and therefore sends visual impulses, to one side of the brain only. The right eye of such an animal, with its own independent pupillary and ocular movements, and possessing a detached right-sided visual field, is connected by its optic nerve only to the left side of the brain. The optic nerves from the two eyes have, therefore, to cross or decussate before reaching the brain.

Total decussation, where each optic nerve passes entirely to the opposite side of the brain, is the condition found in all the lower vertebrate classes. It is also found in those mammals having separate monocular visual fields, absence of consensual reactions of the pupils and of conjugate movements of the eyes.

But as combined monocular fields come into existence and conjugate movements begin to be evident, the totality of decussation ceases. In rabbits a very few fibres of the optic nerve have been found not to cross the mid line at the decussation of the optic chiasma; these few fibres from each eye proceeding to their own side, instead of the opposite side, of the brain.

In this way there is initiated a process by which the visual fields are not separated in their cerebral areas of representation, and the pictures derived from the two eyes are becoming blended in their central termini.

In the ungulates about one-sixth of all fibres of the optic nerve of one side turn to the brain of that side, the remaining five-sixths crossing at the decussation in the chiasma to the opposite side. In the carnivora somewhat more than one-sixth of the fibres pass to their own side of the brain. The evolution has passed from a condition of complete decussation to a condition of *partial decussation* of the optic nerve. In Man, one-half of all the fibres of the optic nerve pass to the brain on the same side and the other half decussate at the chiasma and pass to the opposite side of the brain: there is, therefore, in man a condition of *hemidecussation* of the optic paths.

Now this business of the decussation of the fibres of the optic nerves is no haphazard one. At first all the fibres from each eye pass to the opposite side of the brain. Next, some few fibres from the left side of the left eye pass direct to the left side of the brain and, similarly, some few from the right side of the right eye pass to the right side of the brain, all the remainder crossing. In the final stage all the fibres from the left side of the left eye go direct to the left side, and all the fibres from the right side of the right eye go direct to the right side of the brain. We have, therefore, arrived at a condition in which to the left side of the brain all the fibres derived from the left side of both eyes go, and to the right side of the brain the fibres from the right side of both eyes.

Thus we may say "the visual impressions received from the left halves of the two retinae are superimposed on the left occipital cortex, and those from the right halves of the two retinae on the right occipital cortex" (Treacher Collins).

In this attainment of binocular vision, with consensual reactions of the pupils, conjugate movements of the eyes, hemidecussation of the optic nerves and superimposed cortical rerepresentations, we have the basis for true binocular, stereoscopic vision. The appreciation of form, of contour, of relief and of distance is attained. The picture ceases to be flat, and a vast flood of educational possibilities is begot regarding the exact nature of objects falling within the range of the binocular vision. Binocular stereoscopic vision for distant objects is a great educational gain; the visual world takes on new possibilities for the animal, since visual knowledge of everything seen becomes so much more complex, so increasingly complete. The animal is permitted to realize the positions of objects in space, and to conceive the spatial relations of its own body. There is the dawn of philosophic vision as distinct from the process of merely seeing.

But another step is still to come, and this last stage is brought about when the mobile, inquisitive hand is employed for holding and for examining objects that are brought under the focussed attention of the eyes. When a novel object is taken in hand, there are brought into play all the precise muscular movements of the hands and arms employed in its manipulation: there is evoked that complex sensibility of the hand and arm which tells of the weight of the object; and the sensitive fingers learn of its texture, its temperature and of its consistency. Moreover, its form may be estimated by the dual sources of information of the exploring fingers and the examining eyes. Weight, texture, temperature, consistence and form, as estimated by the touch of the hand, may be correlated with the visual impressions derived from the eyes. Here is a basis of real knowledge of external things. Meanwhile the attention of the eyes is centred upon the object, and there are brought into play the fine consensual reactions of the pupil, the minute adjustments of the ciliary muscle and the lens in accommodation and the conjugate movements of the eyes in the process of convergence. When all the fine ocular adjustments are made and the eyes are fixed with attention upon the novel object held in the hands, the image of the object falls upon one definite area of each retina—the *area centralis retinae* (see Figure 76). This area is one of special sensitiveness and in its more perfect form, which is not present in the lemurs, but is found only in Tarsiers, higher monkeys, anthropoid apes and man, it is specialized as the *macula lutea*. In the macula lutea or yellow spot only those most specialized sensory elements—the cones—are present. It is said that 7,000 cones are crowded together in the centre of the human fovea and it is there that the maximum acuity of form sense and colour sense has its seat. We may, therefore, say, that the accessory factors that have led to the attainment of the sense of vision, such as we know it, have been brought about mainly by the emancipation of the fore-limb and the use of the mobile sensitive hand. Step by step we have acquired binocular vision, consensual reactions of the pupils, conjugate movements of the eyes, hemidecussation of the fibres of the optic nerve and dual cerebral representation of the two retinae. In this way has come stereoscopic vision and in its train has followed the development of a fixation field, the perfection of a specialized area centralis as a well-defined macula lutea with a fovea centralis. Vision with us is not only binocular; it is, for the attentive examination of objects near at hand, bimacular; and with bimacular vision there develops the perfection of form sense and colour appreciation.

That we should thus appropriate colour vision for ourselves and the members of our immediate phylum, may seem to some people to be unjustified. There are so many commonly observed phenomena which appear to demonstrate the fact that the familiar lower mammals possess colour vision. Does not red excite a bull? We have sounded a caution in connection with the wonderfully acute perception of minimal movement that is undoubtedly possessed by the majority of lower mammals. A similar caution is needed in regard to their high appreciation of degrees of luminosity, and luminosity is an essential part of colour. A colour-blind person can distinguish colours by their varying degrees of luminosity, he may not be able to conceive what normal persons mean by red and green, but he can distinguish red from green if the luminosity of the two colours is different, as we would distinguish two greys of different luminosity. That any of the mammals lower than the monkeys can appreciate colour as apart from luminosity there is no evidence whatever and we must, therefore, conclude that they know not of colour in its aesthetic sense. Indeed we might almost infer this since most mammals are themselves soberly coloured, the monkeys alone showing any high degree of pigmentation distinct from mere pattern of the coat. If any mammals should prove to be the rivals of the Primates in possessing colour vision, it is most likely that they will be found among the squirrels which live in the tree-tops, hold their food in their hands, and are for the most part brightly pigmented. To deny colour vision to the mammals is not to deny it to vertebrates lower in the scale, since it is an undoubted possession of birds and possibly of some reptiles, amphibia and fish, but into the perceptions of these animals we are, as we have previously noted, unable to enter by reason of their different types of cerebral architecture. In the case of man we may go a little further in probing the elements of colour vision, and first we have to realize that it is the last attainment of perfected vision and that perfected vision in our phylum does not mean sense organ perfection but perfection of the pallial visual area. Having regard to the phylogenetic story of vision there is every reason to suppose that colour vision was the outcome of pallial rather than retinal elaboration: and despite the numerous theories to the contrary, there is much evidence in favour of this. A colour-blind person is probably colour-blind with his brain not with his eyes.

CHAPTER XLIII

THE TRIUMPH OF THE PALLIUM

That some small and lowly mammal with a long, sensitive and mobile snout should have so far probed the world with its nose as to gain cortical awareness of its muzzle region may not seem to have been a very great gain for the phylum of which it was an early pioneer. But in truth it was a great attainment: an asset so immense that some of the earliest mammals invested the whole of their cerebral capital in it, and neglected the perfecting of other channels of education. Long ago the monotremes appreciated the vast gain that came from the possession of a sensitive muzzle region, they specialized in its development and, like all specialists, became slaves to their specialization. The Platypus is left with its highly sensitive beak: Echidna retains its wonderful rhinal probe. The monotremes survive to-day as unprogressed specialists, unaltered monomaniacs, who gave up all else that they might perfect sensitive muzzles.

But the more generalized mammals avoided this snare and we have seen that, in our phylum, the cortical representation of the body spread from the muzzle region to other parts of the body in a very definite manner: a manner easy to appreciate when we study the life habits of that great assemblage of the primate phylum which early acquired an arboreal habit.

From awareness of the snout region to awareness of the whole of the body was a progression naturally enough come by in the procession of the Tree Shrews, the Tarsiers and the higher Primates. What this led to in the more purely physical aspects of cerebral advance we have already seen. The whole body gains pallial representation. There comes about a realization of all our parts as entities projected in space: there comes about a deliberative awareness of our physical structure and with it the possibility of performing deliberative and considered movements of all those parts of which we have cortical awareness. In this great gain lies the typically human quality of sensation and the typically human quality of movement. But great though this gain was, it was trivial compared with that which followed in its train. That the great function of the nervous system is the integration of all bodily phenomena is the basal thesis that we owe to the genius of Sherrington; but I fancy we have not yet fully realized the great rôle of the nervous system as the integrator of the more psychic side of human activities.

We have seen that it is somewhat disappointing that so little in the way of function has ever been brought home to the corpus callosum. We know the huge gain it conferred upon the phylum that perfected it, but experimentally it seems to do no more than correlate the two sides of the body and at the most those human beings who have lacked it have only been described as "a little queer" (Cameron). Nevertheless the disappointment at these findings is unjustified: for the functions of the corpus callosum are such as are not easily demonstrated in lower animals, nor ascertained by casual inquiry concerning a person in whom, after death, it has been found lacking. For us the corpus callosum is the expression of the last great integration—the anatomical structure which, in its complete human development, effects unity in the pallial awareness of the individual.

We may say with justice that an elephant knows little of its hind legs: no baby elephant can serve the human infant's apprenticeship of playing with its toes. Little by little in the dawning pallial life of a child comes this awareness of its body: little by little its knowledge is increased until it is integrated into a whole and the child realizes that it is an entity. Awareness of the whole body is the summation of this physical knowledge—realization of an individuality is ultimately its psychic integration. There comes a day in the life of every developing child when it realizes that it is a thing which it is accustomed to know as "I"; it has awareness of its psychic individuality. Many of us can well remember the dawn of this integration of psychic awareness. It may come with some suddenness. It may happen that the realization of the ego is a startling revelation, and many questions, to which there is no answer, may come insistently to the child. It may be a perplexing thought that, had I not been Mother's little boy, but the little boy of the lady next door, should I have been I? There being no ready answer forthcoming—either from the child's own speculations or from the interrogation of its parents—such problems are commonly soon abandoned. Nevertheless, the dawn of the knowledge has created a new era in the psychic life of the individual. It is aware that it is a definite and distinct individuality living in a world peopled by other individualities.

We have realized that, when a movement is initiated from a lower level centre, a stimulus comes into the central nervous system and an impulse goes forth and nothing is left behind. In such a case an animal performs an appropriate movement but it cannot be said to know what it is doing, nor what it has done.

We have also appreciated the fact that when movement is initiated from the pallial level, it is the result of a previous awareness and is a deliberative and considered response. With the pallial initiation of the movement of a part of which we have cortical awareness we may be said to know what we are doing with the part. We deliberate our action, we appreciate it in the doing, we know what we have done. We are conscious of our movements. We are capable of remembering our movements long after they have been accomplished. We are able to consider future movements in a purely abstract manner. A child may unlock a door by using the key, it knows what it is doing when the act is performed, it can remember its movements afterwards, and it can picture itself repeating the action on subsequent occasions. This for an individual action.

When we come to consider the great question as to what is conduct we shall find it is impossible to conceive of conduct except in terms of action. Conduct is a complex of actions.

Now in that great day when the child integrates the elements of awareness into the concept of its own individuality it is on the threshold of the greatest problem that confronts mankind. It is now not a question of a hand or some other part performing actions—it is a question of an individuality acting in relation to other individualities. It is now: What am I doing? What have I done? What shall I do?—and this in relation to the other individualities with which I come into contact. We have integrated the elements of our awareness into the concept of the ego: we have integrated our deliberative actions into a scheme of conduct appropriate to the ego in relation to other egos.

We may say that the human consummation of this process of higher level usurpation, which culminates in pallial reception and pallial initiation, has resulted in the production of that degree of human adjustment of conduct to the demands of a human environment.

Without going back to the early days of the nineteenth century and dallying with the doctrines of Gall and Spurzheim, we may well inquire if, since this business of humanly adjusted conduct seems to be so obviously a pallial function, there is any region of the cortex which is in any special way related to it. We have seen that the badly named motor area of the human cortex is situated about the region of the pre-central or pre-rolandic gyrus. This motor area is, in the lower mammals, situated almost at the anterior extremities of the cerebral hemispheres. In the Tree Shrews and in the Tarsiers there is very little cortex in front of the motor area of the brain. But as the arboreal primate phylum is ascended this *pre-motor*, or *frontal area* of the cortex steadily enlarges, and it may be said with justice that the great outstanding feature of the human brain is the immense size of the cortical field lying anterior to the motor centres (see Figures 22 to 27). This frontal cortical area is, for the most part, a silent field, for no motor response is produced when it is stimulated by the ordinary methods employed in experimental neurology. Since it is an outlier of the motor area, and is developed hand in hand with the increasing specialization of this area it seems not unlikely that it may be an association field of the centre for deliberative movement.

As such it would appear likely that it was concerned with that extension of the production of deliberative movement that we have termed humanly adjusted social conduct. So much the very ordinary deductions from comparative anatomy would seem to render probable. But it is not safe to assign function to structure merely upon such deductions, reasonable as they are. It remains to inquire if there is any physiological evidence as to the functions of the great silent frontal field of the cortex. It may be that upon this point experiments upon animals have led, not to the discovery of the truth, but rather to its obscuring. From a vast number of experiments upon dogs and other laboratory animals no very clear concept of the functions of the frontal area has emerged. It is usually postulated that it is an area concerned with movement and in which is lodged some such factor as attention: but even in the dogs upon which Bianchi made such extensive observations there seems to have been more than mere attention lacking after the removal of the area. With man the results would seem to be far more definite and this is only reasonable when we consider the essentially human nature of this perfected field. Leaving aside the classical crow-bar case, and others concerning which the entire history of the patient before and after injury to the frontal areas was imperfectly recorded, there are the innumerable cases of frontal injuries recorded during the European war. Moreover the findings in cases of encephalitis affecting the frontal portions of the cortex seem clear enough.

In the normal human being the answer to that ever-insistent question—What shall I do? is provided after an interval appropriate to the circumstances. In human beings departing only slightly from the normal there may be more or less than the deliberation that suffices for the truly normal. An individual may be normally prudent, more than normally prudent, or less than normally prudent, as we would say in reviewing the conduct of our fellows. A problem of conduct may be readily solved by one, it may be a burden to another, it may not even appear as a problem to a third. I may see a tie in a shop window, I may decide quickly that I like it, that I need it, that I have the money to purchase it, and that I am doing no wrong in spending my money in that way. Another person, only slightly departing from the normal, may have to visit the shop window many times, may have to go over his accounts and speculate upon variety, necessity, utility and whatnot, before the purchase is made. Whilst another may not even consider if he likes it, if he needs it, if he can afford it, nor even if he has the money in his pocket, for he will go straight in and purchase it. Passing from the normal to the definitely abnormal there are those who when they wake in the morning debate if they shall put on their thick or their thin socks: they will rise with the question still unsettled: they will sit on the bed and debate the matter with themselves and finally fail to complete their toilet because the problem is for them insoluble. Such people are mostly in institutions. Again at the other extremity are those who act entirely on impulse on all occasions, and for whom a considered line of ordinary social conduct is quite unattainable. In lesions of the frontal area this is the type of conduct that is produced. The patient is incapable of considering, of weighing, of deliberating his actions—he acts on impulse. Now gross deficiency of conduct is the hallmark of true insanity. It was Charles Mercier who, with true insight, said "insanity is a disease of conduct, not of intellect"; and in its most pronounced manifestation we may say that impairment of the functions of the frontal areas produces that loss of deliberative human social conduct which demands the isolation of the patient and which is known as mental alienation.

Awareness then has led to this: that it has given us a typically human attribute of the considered actions of the individual towards its human environment. It has given us what we know as human social adjustments of conduct; and the special pallial seat of this human attribute is in that typically human region of the pallium known as the frontal areas. We have a prejudice against people who have retreating foreheads that may or may not be justified: but at least we know that when the anterior areas of the human pallium are injured or deficient the individual is apt to fall short of the ordinary working human standards of socially adjusted conduct.

PART II

CHAPTER XLIV

OUR ORIGINAL EQUIPMENT

In describing the nervous mechanism of the human body Herrick[1] has attempted to convey to us some idea of its almost infinite complexity by stating that a complete map of all the circuits of all telephone and telegraph lines in North America would be simple in comparison with a chart, if it could be drawn, of the nervous arcs and circuits in the human body. Obviously, then, the human machine does not constitute the best starting point for studies of nervous mechanism. The problem would look too appallingly complicated. We must examine simple and still simpler organisms until we go clear back through all the vertebrate and invertebrate systems to the lowly but ubiquitous unicellular structure. To understand human conduct we must pick up our first threads of comprehension by examining the behaviour of microscopic organisms living in myriads in a pool of water, and propelling themselves across the surface of objects by queer grasping, rolling, or suction movements.

Just as the anatomist, according to his point of view, may regard this little mass of living matter as all-nervous or non-nervous, so the psychologist may regard it as all belly or all mind. To our point of view the characterization is immaterial. The amoeba presents to our consideration the simplest kind of structure and the simplest form of behaviour. The important fact about this speck of protoplasm is that it is *alive*. We too are alive and our infinitely complex structure and our wonderfully varied behaviour have as their basis what the microscope may tell us of the structure and behaviour of these minute organisms. These too were our beginnings and from the standpoint of the understanding of ourselves we may say that the proper study of mankind is the amoeba.

---

[1] *Brains of Rats and Men.*—C. Judson Herrick.

But though we have gone but little further than a very casual mention of this primitive organism we have already given ninety per cent. of all possible description of its behaviour by stating the simple fact that it is alive. Many books, involving many years of patient observation and research have been devoted to that remaining ten per cent of explanation. But to fill up the balance of understanding, the huge gap of ignorance that we conceal when we talk about "living", would involve the understanding of the interaction of all the forces of physics and chemistry that brings about life. Some day men may approach nearer to this understanding, but that time is not yet.

Having admitted our vast ignorance of those mysterious processes in Nature which, working together for countless aeons of time, have resulted in the product which we call life, let us begin our task of observation and description at the only possible point—with the speck in being, the machine in action, the living cell.

The first question which we must answer is—how do we know that it is alive? The reply that the microscope enables us to make is that it moves. So too do inanimate particles of matter, which not only move but in certain conditions apparently seek one another and combine in various ways. But there is an essential difference between the movement of living and non-living matter. The movement of inanimate particles is in response to forces impelling them towards a state of equilibrium or rest. Once having reached this state they will not move again unless in some way this equilibrium is disturbed. Once the stone has reached the bottom of the hill or the bed of the sea it will roll no further unless lower depths open beneath it. It is inert, at rest. Once the tension of the spring is wholly released it will cease to unwind. But living matter in its movements is essentially different from the rolling stone or the spring or the chemically attracted atoms, for it carries on movements whose end or purpose is not equilibrium or rest, but more movements. Its life activity is self-initiated, its springs of action are within itself. Immediately it has permanently lost this capacity for self-initiated movements or immediately it has come to a state of permanent enforced immobility, then the creature is dead. Its substance may still move, but inanimately, the sport of the winds or tides.

The behaviour of a living organism may therefore be summarized as an inherent tendency towards continued movement or activity. During periods of rest this activity may seem to have ceased, but it is only the appearance of cessation. The life processes are still going on though they may not be expressed in overt action. When we use the word inherent we are covering up by the use of the term much of that large fund of ignorance, that ninety or more per cent of life of which we can give no explanation. It is only the tendency towards constant movement that we can observe and more or less adequately describe. How or why it comes about is beyond our ken.

Even within the limits of this comparatively simple description of the behaviour of a living organism there is room for all kinds of philosophical and psychological objections, and a general befogging of the issue by the use of longer and worse words than those which we have employed. In insisting on the tendency of the living organism towards continued activity we are not emphasizing any more than the bare facts of observation, but in so doing we part company with one of the recent schools of psychologists who regard the life tendency as being directed towards equilibrium. But as it is the movements of protozoa with which we are concerned rather than with movements of psychological thought we will adhere to our original description. As an elaboration of our original statement we find that in the pursuance of this tendency the organism resists by every means in its power anything which threatens its continued activity, and conversely seeks by every means in its power things or conditions which will further the continuance of its activity. Keeping these facts of the behaviour of the amoeba in mind, we need not attach any particular significance to the distinction which is sometimes made between the actions of approach or withdrawal, which are merely the negative and positive aspects of the one tendency. There is no need also to distinguish sharply between movements of locomotion and movements in response to special stimuli. Whether they be negative, positive or food-taking reactions, or the peculiar set of movements enacted when the amoeba becomes detached from a solid surface, they can all be subsumed under one purposive tendency. In the last-named conditions of detachment from a solid surface the detached organism sends out in all directions greatly elongated pseudopodia until one of these comes into contact with a solid surface to which it attaches itself, the whole animal following and then taking up again its ordinary form and locomotion. This conduct is a good illustration of the amoeba's tendency to seek the condition in which its self-directed movements are possible, conditions which are absent when the animal is unattached.

Perhaps at this point it would be well to describe the life activity of the unicellular organism in a little more detail. We may take *Amoeba proteus* as a commonly observed example. It is a very tiny speck of protoplasm containing a nucleus and little sacs or vacuoles, and as we have mentioned, it moves about the surface of objects in the water by projecting part of its body protoplasm in advance of the rest of the cell and then withdrawing this and sending out other pseudopodia, as these processes are called. The currents of protoplasm in the cell body have been variously described by different observers, but the actual mechanics of the amoeba's movements need not be discussed here. It is interesting to note, however, that the amoeba will carry out movements of avoidance if it meets with a current of water of a different solution from the one to which it is accustomed. It will also carry out these avoiding movements if it is heated on one side or if it comes into violent contact with a solid body other than that to which it is attached, or if it is subjected to strong light or an electric current. It will also, if hungry, move towards food and has been observed in the apparently determined pursuit and capture of another of its own species. The food-taking reaction consists of an envelopment of the whole object within its own body, followed by an ejection of the undigested portion. It may be said to flow around its prey. It can be fooled into ingesting indigestible carmine grains and will even swallow particles of ground glass if these are in motion.

The reproductive process in amoebae is interesting. It consists in some species of binary fission in which the cell literally splits into two halves, the offspring being entirely similar to the original cell except in size. We cannot speak of the original cell as the parent since in the dividing process it loses its identity and disappears. Reproduction in this case is merely a division of the original life capital and a reinvestment of it in two new organisms. The amoeba evidently is disinclined to keep all its eggs in one basket, so to speak. Aside from the ordinary accidents of Nature, such as starvation, poisoning, or falling a prey to some other animal, the amoeba is immortal in the sense that the experience of the new amoeba is continuous with that of the original undivided cell. This production by binary fission is apparently a biologically advantageous proceeding since the chances of survival of the two new amoebae are twice that of the old one from which they were derived.

In its other mode of reproduction the factor of biological advantage is even more apparent. In times of scarcity or enforced inaction, as in winter, the amoeba becomes a rounded mass by drawing in its pseudopodia and in this condition lies dormant, the vital processes being in abeyance as it were. Thus it can survive drying or freezing. But that life is not absent is shown by the fact that at this time the nucleus often divides until a very large number of nuclei have been formed. These, when they escape, form young amoebae, the main differences from the adult being those of size and shape of pseudopodia which are elongated and pointed, a condition favourable to assuming a new location. Here again the identity of the original cell is merged in that of the young organisms and by this process of nuclear division survival chances are multiplied to a great extent.

The important points to remember when we consider reproduction of the amoeba is that it is a process carried out by one individual cell only, and that secondly it is of biological advantage to that cell. Later on in the stages of development there came about a differentiation of function in multicellular organisms, making reproduction by fission impossible or disadvantageous. It was then a necessary development to have cells set apart whose business it should be to carry on the generative process. Following this came a stage when it became advantageous for two individuals to share this business between them and so have a division of the sexes. This sexual division undoubtedly was due to a conflict of two opposing tendencies in the reproducing instinct. In order to ensure the continuance of the species the generative impulse had to be accentuated in behaviour, or in other words the organism should be rather continuously sexually active. But the process of reproduction once under way required time and a certain cessation of sexual activity. Nature therefore found it advantageous to separate these two rôles in different individuals, giving sexual activity to the male, and sexual passivity to the female. The male can then spend his time and energy in seeking and pursuing the female, and the latter can conserve her time and energy for producing the young.

Bearing in mind the fact that reproduction by fission was originally advantageous to the individual and that sexual reproduction was a necessary accompaniment of increased complexity of structure and function, then we may regard what is called the reproductive instinct as a development of the basic tendency that we first postulated —the tendency of the living animal to continue its life activity.

That reproduction of young is of biological advantage in another way may be simply illustrated by the extremely lavish scale on which Nature carries it out. In organisms which are the prey of other organisms the chances of individual survival are greatly enhanced by over-production. This is exemplified by the shoal of fishes. This habit of going in swarms is of no defensive value except for the fact that there are more fishes in the shoal than their enemies can possibly devour. The individual fish hides behind a screen of its own kind and if it does chance to survive it has saved thereby the energy which otherwise it would need to employ in efforts to escape. It should be noted in passing, however, that over-production is only resorted to by comparatively small animals or those that live where food is exceedingly abundant and never-failing, conditions commonly to be found in the sea and in the foliage of great forests. Otherwise over-production would prove a two-edged sword. In gaining a biological advantage by reproducing in vast numbers and thus glutting the appetites of the enemies of its species, the animal would be brought, because of the failing food supply, into conditions of keen competition with its own kind.

If some such principle of biological advantage did not originally underlie the reproductive impulse it would be difficult to explain it on any other grounds than as an altruistic interest exhibited by the individual in the welfare of the race or species to which it belongs. If we can conceive of the reproductive process as being in the first place self-reproductive and therefore self-preservative it is much more understandable and may be regarded as a manifestation of that basic tendency towards continuance of life activity.

Even when we reach the multicellular stage of development where there is a division of labour, a differentiation of function, this basic tendency remains a characteristic of the differentiated cell or group of cells. Whether their business be the secretion and appropriate discharge of digestive fluid, the secretion and discharge of spermatic fluid, or whether their business be the gathering and appropriate transmission of sensory stimuli as nervous impulses, the tendency of the cells or cell groups is always to continue their activity. If this activity is being hindered they have the right to make their complaint heard throughout the whole organism and to enlist its whole energy on their behalf. When we are very hungry, for example, it is not only the digestive organs but the whole body which is in distress.

Summarizing this chapter we may say that there is a constant struggle for existence and the response of the organism is many sided. Life always seeks to maintain itself. To explain how it does so is partly the business of anatomy which describes the animal structure and partly the business of physiology and psychology which describe the behaviour, or the function, whether it be physical or mental, which is dependent on that structure. This behaviour always may be related, directly or indirectly, to the one basic tendency, the tendency towards continued activity which living matter displays. The original self-preservative tendency has, it is true, irradiated so that it is no longer centred in individual welfare but has also been concerned with the welfare of the race; but nevertheless there is one basic tendency and not two. The tendency towards self-expression which some writers consider basic is in its many and various phases merely part of the general tendency of the cells to continue that activity for which they have been set apart. If they have been set apart for the business of display, then display activities are their business. The building up of what we call personality and character is the attaining of a proper balance in the activity of the differentiated cells. It is the insuring that the demands of any part for the furtherance of its activity are duly proportionate to the purposes of the whole organism.

The selection of the amoeba as the starting-point for the consideration of human behaviour is a more or less tacit acknowledgment of the principle that in the development of the animal kingdom nothing which is entirely new or *sui generis* has been added. In no animal, no matter how highly constituted, is there anything either in structure or behaviour, the germs or beginnings of which are not to be found in simpler forms of life. Hence even faith, hope, and charity are merely the ends of an evolutionary thread which stretches back through all the generations of all the species and have their inception in the behaviour of the protozoa. This book is an attempt to pick up some of the fibres of that thread and to discover how they are interlaced.

CHAPTER XLV

BIOLOGICAL PATHWAYS

If we were to recapitulate our observations of the amoeba's behaviour, using the same descriptive terms that we would apply in similar circumstances to our own actions, we would say that *Amoeba proteus* does not like to bump unexpectedly into solid objects or to be prodded or pushed or pricked. It also has an aversion to bright light or heat, or electric shocks or to a current of water which is different from what it has been accustomed to live in. Its main interest in life seems to be the getting of food for itself, and things that move are the things which it desires to investigate and if it is hungry and they are of suitable size, to pursue, capture and devour. It has been seen pursuing a smaller amoeba with considerable persistence, eventually catching it and partly swallowing it, only to have its prey wriggle free and finally escape despite a renewed pursuit. It has apparently a certain degree of ability to learn by experience. This is shown by the fact that after being fed for a time with indigestible carmine grains its reaction changes and it comes to reject them as food. In the same way it shows some ability to get used to a new situation since it will, after first reacting negatively to a change of water, resume after a time its normal behaviour.

But in using such terms as "aversion," "like," "interest," "learn," etc., we cannot accept them as connoting the same mental processes as when we apply them to human behaviour. They may be used as a matter of convenience of description but we must remember that they cannot possibly mean the same things when applied to the conduct of a simple one-celled animal as they do when used to describe the behaviour of a wonderfully complicated organism such as man. The behaviour itself may not differ greatly in amoeba and man but its underlying basis is entirely different. Man too has his likes and dislikes, his attractions and his aversions, and strangely enough he has an aversion for most of the things which the amoeba avoids. But the reasons which prompt man to action, the reasons why he pursues or avoids are infinitely more varied than those which actuate the amoeba. Man may pursue an object for love, for hunger, for spite, for vain glory, for health, for fun, for sheer cussedness or a dozen different reasons. Hunger seems to be the dominant drive to action in the amoeba and it probably knows little or nothing of the rest. Then of course, the things which the amoeba does are extremely simple and restricted in variety and scope whereas man's repertoire of actions is wonderfully full. Then another fundamental difference is that when man pursues an object he always knows that he is pursuing, often he knows what he is pursuing and sometimes why he is pursuing it. In these three kinds of self-knowledge the amoeba probably shares only to a very limited degree. It will probably be aware of an organic sensation such as hunger as a motive to action; it will also have an awareness of movement, and it possesses some means of detecting movement in other organisms. This dim awareness, sketchy and rudimentary though it be, is undoubtedly the basis of all the external and internal sensations, the satisfactions and dissatisfactions which we as human beings experience. It is perhaps worth while to reiterate that the whole gamut of action whether it be that of amoeba or man is the expression of the one basic tendency in living matter, the tendency towards continued activity.

The question as to whether or not an amoeba possesses anything akin to mind and knowledge is an exceedingly engrossing one, but since we have not sufficient facts at hand to admit of even a tentative solution we may pass on to a further analysis of its known behaviour. A sure inference that we can draw from watching its microscopic advances and withdrawals is that it is sensitive to things outside itself. Light and heat and the presence of food are reacted to in exactly the same way by all hungry amoebae, but of the many things which might be reacted to in the animal's environment certain things only seem to be selected, and out of several ways in which the animal might react it seems to choose only a certain negative or positive form of response. The responses are by no means dictated by blind chance. Any of these single stimuli will call forth its own proper response. How has this remarkable uniformity of reaction come about? These actions or responses have not been learned by the individual animal and it has not the sense or senses to imitate the actions of other amoebae. How can anything be learned which has never been taught?

Before trying to answer any of these questions we wish to note another thing about the behaviour of the amoeba. When two stimuli, each of which has its proper specific reaction, are presented at the one time, as for example the presence of food in a lighted area, the reactions to which are ordinarily opposite, which reaction will the animal choose? It will depend entirely on the internal physiological state of the animal. If it is very hungry it will respond positively by advancing, if not, then negatively by withdrawing. In other words even at this level of existence the animal is not entirely at the mercy of its environment. It is not merely mechanically responsive in the same way as the ninepin or the group of ninepins is to a blow. In each total situation that faces the animal something from its own internal organization enters. In other words there is a merging of the animal's internal and external environment to form a situation. The pattern, the configuration, the background and hence the situation itself constantly changes even though the elements in it remain the same. To an amoeba a moving carmine grain presents a situation entirely different from that afforded by a stationary one; and to a hungry amoeba and to one that is well fed, the situation will also be entirely different. A moving carmine grain plus the animal's hunger constitute a different situation pattern and call forth a different response. The environmental situation into which something from the animal itself does not enter is irrelevant, and strictly speaking, is not the animal's environment at all.

Stimulus and response, therefore, together form the action pattern of the animal. That which cannot be responded to is not a stimulus to the animal and does not become any real part of its environment. The pictures on the wall of the room form part of our environment, but are outside of the behaviour patterns of the goldfish in the bowl. The animal's structure and behaviour are therefore factors in determining the range of its environment. Insistence on this point of view is rather important as it prevents us from thinking of the reactions of an animal to stimuli as being comparatively simple affairs. We must take into account the further fact that the structure of the animal determines the arrangement of its environmental patterns. Behaviour is not, therefore, even in the lowest animal, a matter of the presentation of a stimulus followed by an inevitable response. There is an element of choice in the proceeding. The amoeba chooses to eat or not to eat, but its choice is dictated by its belly and not by its mind. There, perhaps, is the fundamental difference between the behaviour of the man and the amoeba. Man's choice in many respects is dictated by his cortex and the difference between man and the higher animals lies in the number of situations into which the dictation of his cortex enters rather than his stomach or lower nervous centres.

After this somewhat philosophical digression we must come back to the question we originally propounded—if amoebae have not minds how does their apparent uniformity of response come about? Why do they all choose to react in the same way? Why should they all react negatively to a beam of strong light or an electric current? There may be slight differences in behaviour due to slight variations in structure, but these are so insignificant that they cannot be detected, so that we are warranted in speaking of the amoeba's behaviour as being uniform, and it is this similarity of response for which we must account. The only explanation possible—since the animal does not learn by individual experience—is that its reactions are inherited, handed down as the sum of experiences of countless amoebae to which directly or indirectly our particular specimen is related and from which it was derived. As we have seen in examining its methods of reproduction the experience of an amoeba is continued from one organism to the two or many into which it divides. But this process of handing on experiences depends on the assumption that every situation reacted to by the animal leaves some kind of trace, some change of chemical structure which facilitates the same kind of response the next time this situation presents itself. Just what this facilitation consists of we do not know, but in its operation it resembles the effect of a drop of water trickling down a dusty window pane. It leaves behind it a surface film of water that renders the passage of the next drop down the same course so much the easier. Even if this surface film is allowed to dry, the passage of the next drop is still facilitated because of the rearrangement of dust particles along the course. Now this is a purely mechanical analogy, and whether the chemical constituents of the cell are rearranged by the passage of a stimulus and the carrying out of a response, or whether there is actually something left behind in the organism we do not know. But this facilitation is the basis of what at higher levels of animal functioning we call "memory" so that there is no valid objection to speaking of the process as the memory of the cell. It does not differ in essence from what takes place when we carry out some well-practised or automatic action. The stimulus, whatever it may be, proceeds along some well-worn nerve path, so to speak, and the muscular reaction follows in its accustomed sequence. But the difference between our remembered action and that of the amoeba is that ours is an individually learned reaction while that of the amoeba is racially learned behaviour and is the product of all the experience of all the amoebae. To distinguish this process of racial facilitation from individual learning we shall refer to it as biological memory. It is that process which enables the amoeba to draw on the past experience of all the amoebae as a guide to its action. This handed-on experience is sometimes called instinctive behaviour, and the difference between these sequences of action and ordinary habits is that the latter are built *up* during the lifetime of the individual and instinctive reactions are built *in* during the lifetime of the race. But we must always remember that both habits and instinctive behaviour rest on the same mnemonic basis, more or less permanent modification of structure or chemical composition of the cell by behaviour.

When animals reach the multicellular stage and reproduction is no longer a matter of fission but the business of specialized germ cells, there must still be continuity of experience or else the built-in habits of the race or species will be lost to the new individual. Obviously, considering the results of individual growth and development the body of the parent cannot be continuous with that of the offspring. Nature has provided for the handing on of the experience of the race by making the germ plasm continuous. It, like the amoeba, is immortal, barring the accidents of Nature or the event of the individual in whose body the germ plasm is stored failing to find a mate. Immediately the union of two germ cells has taken place and cell division begins, the new germ cells are set aside and have their own cycle of development. The way in which the biological memory or the experience of the species is represented in the germ cell is a mystery to us at present. The study of the way in which this representation in the germ cells affects the growth and behaviour of the future organism is the study of heredity.

Considering the relative structural simplicity of the amoeba—a speck of protoplasm with a nucleus—its behaviour is remarkably varied. How have its life habits been built up? Did the original amoeba exhibit the same aversions and attractions as those exemplified in the behaviour of these organisms to-day? Probably not, for that would assume no progress at all for this creature since the dawn of life. In all likelihood the behaviour of the first amoeba was considerably more blundering and chance-driven than is that of the amoeba to-day. It seems an improbable hypothesis that the only advances in the direction of improved structure and function are those made when a new form is evolved. Surely some cumulative progress is possible within the structural limits of the same species.

The weight of scientific opinion leans towards the view that advances in development are due to mutations or variations, that is to say, a variability of structure in the germ cells, which, if advantageous to the animal, is fixed and transmitted in the descendants. But we must remember that the improved structure is the end result and that it must be built up in the individual by the ordinary life processes of metabolism, the material being gained in the ordinary way from the animal's environment. The advantageous mutation takes the form then of a potentiality for adaptation to environment. The adaptation itself is not present but is merely represented in the germ plasm. Now we have seen that through what we have called biological memory the animal's reactions have become set or stereotyped. The only way in which a new adaptation can be made, or in other words behaviour can change, is by a more plastic condition of the germ plasm so that to its already present capacity for building up a certain structure with its associated behaviour patterns, some new potentiality is added. When this plasticity, this adaptability is so increased as to make sufficiently marked differences in structure and behaviour then a new species is recognized. But if it is degree of adaptability or plasticity that is subject to mutation or occasional variation why should not some germ plasm be so plastic as to be affected by the experience of the individual in whose body it is housed and which forms for the time being its environment? If this were possible then it would be easier to account for the building up of the immensely complicated behaviour patterns of the higher animals by small cumulative gains attributable to the life experience of the individual.

The answer that the geneticist gives to the query regarding this possible transmission of acquired characteristics is that it is not possible because in his experience it does not occur. But before we accept this dictum we must stop and realize that this increased plasticity of the germ plasm, this potentiality for new adaptations in the behaviour of the structurally complete or mature descendant, must surely occur very rarely, or else we should be confronted with a bewildering riot of new species. It seems as though at times in the history of a phylum there has been a period of variable plasticity resulting in a flare-up of new forms, but this may occur more readily when the species is young and not biologically set in its ways.

It may be necessary to remind the geneticist that he has had but a very brief time and a very few generations of animals with which to carry on his experiments whilst

Nature has had many, many aeons of years and illimitable organisms with which to work. Thirty generations of mice whose tails have been cut off are surely inconclusive evidence that the plasticity of germ plasm cannot be affected by individual experience. At the same time it must be admitted that the theory of inheritance by use has at present meagre support among biologists.

In considering how immensely complicated the mechanism of even our simplest muscular movements is, as for example how a simple reflex action, such as is called forth by pricking the sole of the foot, involves the remarkable and unfailing co-ordination of agonists and antagonists, synergics and fixators among the muscles, one wonders how such behaviour patterns could possibly be built up if Nature had to wait for purely fortuitous mutations to bring them about. It is surely ridiculous to suppose that such muscular habits were born full armoured like Athene from the head of Jove just as it would be absurd to suppose that any of our individual skilled operations could be acquired without a building-up process. To many people a reflex action looks as simple as the raising of a weight by a string passing over a pulley. The pull on the string plays the part of the stimulus, the string and the pulley correspond to the nervous mechanism, and the raising of the weight is the response. But as we have seen in the first part of this book there is no such simplicity in any muscular movement, but a remarkably complex sequence of muscular actions dependent in turn upon an equally complex innervation. When we consider the perfections of this mechanism and how we are literally bundles of such behaviour patterns it is difficult to believe that fortuitous changes in the germ cells are the sole cause.

A great many of these behaviour patterns represent unlearned reactions. However we may disagree regarding the way in which the transmission came about, the fact is certain that the behaviour of any animal of any species is influenced or directed by the experience of all the animals of that species which came before it. Much of our behaviour follows along these well-worn biological paths. We may disagree as to whether we shall call racially built-in habits instincts, prepotent reflexes or whatnot, and may differ even more violently as to how many of them there are, but the settlement of these matters must await not more discussion, as some seem to think, but more observation. As regards these instinctive or unlearned reactions we must be careful not to assume that the animal inherits any specific reactions to specific stimuli. Carmine grains may never before have come within the range of experience of any amoebae yet the animal reacts at first positively towards them. What the animal inherits from the previous experience of its kind is the tendency to react positively, when hungry, to moving particles, although of course it can have no inherited reactions to carmine grains as such. Particles of ground glass will serve equally well as stimuli. Similarly it will react at first negatively to a strong beam of light, not as a specific stimulus but simply as an unusual experience or sudden change of environmental background. This is a condition which racial experience has proved to be one of potential danger and therefore to be reacted to negatively. To think of racial memories as being specific in the sense that individual memories are specific, each situation being recognized as having occurred before and being reacted to accordingly, is to assume a degree of continuity of experience between individual and species which does not exist.

CHAPTER XLVI

SENSES AND SENSITIVITY

In the last chapter we pointed out that the basis of biological progress consisted in variations of plasticity of germ plasm by which the animal structure was capable of wider adaptations to its environment through the building up of more complex behaviour patterns. But this increased capacity for adaptations could only be effected through an improvement of the channels of sensation, the means by which the animal keeps in touch with its environment.

We have seen that the animal in certain situations which are relevant to the continuance of its life activity will react in a certain way. This movement in response to stimulation is, of course, proof that the living cell has two qualities, sensitivity and contractility, or if we wish we may sum up both these qualities by saying that the cell is irritable. In the one-celled animal apparently all parts of its surface are equally sensitive and all parts of the inner substance are equally contractile. But if this equality of functioning were possessed by all cells in the multicellular animal then there would be no advantage in being multicellular. The first result of a number of cells being combined into the one structure will be that the life experience of cells will differ according to their location and that accordingly they will differ in the nature or degree of their response. The cells of the surface being in constant touch with their outside environment will naturally develop increased sensitivity while the cells beneath the surface will just as naturally specialize in contractility. In this way closer touch with the outside world and more effective response will both be furthered.

But these considerations lead us to recognize that in the multicellular organism this division of work between the surface and interior cells will depend upon another quality, viz., conductivity, or the ability to hand on a stimulus. The cells of the surface are the environment of the cells of the interior and the latter must retain their sensitivity as well as their contractility. In short the stimulus from the environment must be communicated or conducted to the contractile cells.

Even in the unicellular animal we may see examples of this conductivity. We have noted that if the tiny amoeba becomes detached from the solid body on which it crawls, it alters its shape so that it has hardly any body plasm at all, almost the whole of its substance being used in lengthening its pseudopodia. As soon as one of these narrow tentacle-like pseudopodia touches a solid surface it attaches itself and soon the whole body of the animal is drawn towards this point. Quite evidently some kind of impulse travelled along the tentacle and was responsible for the subsequent behaviour. As the form and structure of multicellular animals became more complex, this conducting of impulses became more necessary to the unified action of the animal and so the transmission of impulses came to be the special business of the cells which lay along the natural pathways of these impulses.

In animals such as the starfish this communicating system has been developed to such a point as to bring about partial unification or integration of the animal's behaviour. If a rubber band be placed tightly round one of the tentacles of the starfish it will go through various movements directed towards freeing itself from the encumbrance. It may first rub the tentacle against a solid body, then bring an adjacent tentacle into play in the effort to detach it, and finally if all other devices are unsuccessful may even proceed to amputate the offending member. That the integration of behaviour is not wholly perfected in animals of this evolutionary stage is shown by the experiment of feeding filter paper soaked in meat juice to one tentacle of a sea-anemone. After a certain number of trials the tentacle will refuse to accept the filter paper and instead of carrying it to the mouth will carry out movements directed towards getting rid of the paper. When another tentacle is offered the paper it will at first accept it though after a few trials it quickly learns to reject it. Evidently the sea-anemone has proceeded a certain distance towards achieving a communicating system but its nervous structure is not sufficiently well integrated to admit of the whole body sharing equally in the experience of each tentacle.

We find even in comparatively simple animal structures remarkable adaptations of the cells for different kinds of functioning. We see these exemplified in the cells of the surface whose business it is to develop their sensitivity to outside stimuli, the cells of the interior, or the cells which are to carry out adequate responses and the cells which are to form the pathways of communication between sensitive surface and more distant parts so that unified or integrated action will result. This grouping together of cells of like function we have already called "cytoclesis," and this is further exemplified when we find a process of further differentiation proceeding, as when the cells of the surface begin to be grouped according to degree or kind of sensitivity. These groupings form placodes which, as we have seen in the first part of the book, are the forerunners of the organs of special sense such as the eye and the ear. But the most primitive sense is touch and in man the sensitivity of the skin to touch varies in different parts of the body. Extremities such as the tip of the tongue or the fingers are extremely sensitive so that we can detect two points of a compass in contact with the skin even when the points are very close together. On the skin of the middle of the back or of the thigh the points must be inches apart before we can say with certainty whether we are being touched by both points or only one.

How far this differentiation of sensitivity of the cells of the external nervous system has proceeded we realize when we consider the sensory equipment of the higher animals. The very lightest touch which we can perceive on the most sensitive parts of our bodies is not to be compared with the delicate impact of sound waves which we can perceive with the cells of the tympanum of the ear. More delicate still by far is the sensitivity of the cells of the retina to light waves. Even within the eye itself there is a further differentiation within the "fovea centralis" or yellow spot, into which are gathered the most sensitive cells of the eye. At the centre of this spot, our power of distinguishing visual sensations is at its maximum while in the outer parts around the fovea it is less; it diminishes just outside the yellow spot and continues to grow gradually less towards the periphery of the retina.

Incidentally this fact of the varying sensitivity of the parts of the retina forms the basis of a widely accepted theory of colour vision. The Ladd-Franklin theory which is a modification of Hering's theory supposes that there have been three stages in the evolution of the colour sense. In the first stage the cells of the retina responded in the same way to all light waves of whatever length so that the eye could only distinguish white and black. The second stage of development was reached when some of the cells were able to respond to waves of different length. The response to the longest waves gave the sensation yellow and that to the shortest waves the sensation blue. A further refinement of sensitivity took place when the yellow waves were also differentiated according to their length, the longer giving the sensation red and the shorter green. When we blend red and green the two responses are fused and revert to the more primitive sensation yellow. When we blend yellow and blue they revert to the more primitive sensation, white.

Colour-blindness, if this theory were accepted, is easily explained. In red-green colour-blind people, sensitivity development in the retina has only proceeded to the second stage. In totally colour-blind persons the whole retina is still in the first stage of evolution. Though this theory is ingenious, it is not firmly established. There is a good deal of evidence available indicating that colour-blindness may be cortical in origin as well as peripheral.

What we see so well exemplified in the eye is the story of development of the cells of the external nervous system —a development towards extreme sensitivity, a grouping of cells of like sensitivity into placodes and finally the development of sense organs which serve to bring the animal into touch with its more remote as well as its immediate environment. This extension of the range of sense perception has had, as we shall see later, most important effects.

But progress and development have by no means been limited to the cells of the external nervous system. The other parts of the stimulus-linkage-response system have also gone forward. The cells whose business it is to transmit impulses must become specialized for rapidity of transmission. Obviously the animal which can most rapidly react as a whole to any situation particularly relevant to its continued activity will have its chances of survival greatly increased. The business of the nerve cells is to transmit the impulse as rapidly as possible and just as quickly swing back into equilibrium to transmit the next.

The cells which act must be specialized not for extreme sensitivitiy nor for rapid momentary reaction, but for violence of response. Compared with the speed of reaction of nerve cells the muscle cells are extremely slow. True it is that the quickness of our hand deceives the eyes of others but our own nerves and eyes can keep account of the hand's slightest movement. Compared with the sensitivity of the cells of the surface the muscle cells are obtuse and dull. Muscular action in order to be effective must have a certain period of continuance. Extremely rapid reactions would not be of particular advantage to the muscles. Their action must be also proportionate to the strength of the bony skeleton. Too rapid or too violent muscular reaction would perhaps result in the breaking of our own bones. A good example of the limitations of speed of muscular reactions is shown by the tapping test in which maximum speed is soon reached and try as we will we cannot improve it.

In all of this development Nature has not gone a step further than she needs must. The measure of our experience is the measure of our development. In other words Nature gives us as much bodily development as we need to cope with our environment and no more. As regards muscles, because of their slowness to respond, it is very difficult to teach them to carry out new series or sequences of movements. It takes years of practice to enable our fingers to keep up with our eyes, to go where we want them to go. There are other animals besides old dogs which cannot be taught new tricks for, as is well known, youth is the age of muscular plasticity. As regards the nerve cells their rapidity of reaction has its limits. Thought impulses do not travel with the speed of lightning—far from it. On the basis of reaction time experiments, which test in thousandths of a second how long it takes to respond to a sudden stimulus such as a prick of a needle in the foot, it has been found that the speed of nerve impulses varies around 140 feet per second which is about ninety-five miles an hour. Man has learned to propel himself through the air faster than nerve impulses can travel, and can send messages along a telegraph line at an immensely quicker time than he can send them through his own body.

Wonderful as the keenness of our senses appears to be, Nature has by no means exhausted the possibilities of sensitivity. Inanimate matter can be so organized as to display infinitely greater sensitivity. The aerial wire of the radio can respond to stimuli which are the result of sounds initiated many hundreds of miles away. The important distinction between the sensitivity of the living cell and that of the radio receptor is that the stimulus which the latter receives is of no value to the radio apparatus. The stimuli to which the living mechanism responds are those which have actual or potential meaning to it as furthering or hindering its continued activity.

In ontogenetic or individual development Nature is constantly preparing for the future by laying down structures in advance of function. She is able to do this because she has the experience of the race to guide her. In phylogenetic development she has no such leads and racial progress must be slowly gained and consolidated.

The manner in which individual experience sets the bounds of racial progress is realized more clearly when we study our sensory equipment. If a wheel is rotated very rapidly we cannot detect the individual spokes. Even if large objects such as express trains move past us more rapidly than we are accustomed to seeing large objects move in a natural way, then we cannot take in the details of appearance. We know that the particles of any solid object are in constant motion but our eyes do not inform us of the fact. The reason for this bluntness of sensitivity is that it is the wheel as a rotating disc and not as a collection of spokes that is to us the relevant stimulus. We must react to a table as a solid object and not as an aggregation of moving particles. Microscopic or telescopic vision may be necessary for us to use in scientific investigations in civilized life but these needs or uses far transcend those of primitive man and indeed those of the ordinary person in our own community.

Man has dominion over the rest of the animals mainly because he has invented missiles that can move quicker than his victims can see them coming. He may be at the same time the victim of his own inventions. He cannot detect the flight of a rifle bullet and it would be of little advantage to be able to do so since he lacks the motor mechanism that could act quickly enough to enable him to dodge it.

Telescopic vision means extremely narrow range and microscopic vision means an extremely close focus, both of which conditions would have been extremely disadvantageous for man in the ordinary conditions of life. Nature has chosen a new way to make us less directly dependent on our sense perceptions. Instead of keener smell or more acute hearing or better vision, Nature has endowed us with a cortex, the organ which makes experimental procedure possible. In order to make room for a cortex some of man's sensory equipment has been decidedly diminished in comparison with that of the so-called lower animals. The sense of smell has diminished with its diminishing importance so that a comparatively small part of the brain is concerned with this sense. Absent also from man's sensory repertoire is that mysterious sense which enables some animals and many insects to find each other unerringly in the mating season, nor do we possess the sense of direction developed by some birds.

Generally speaking we may say that Nature had gone as far as she could in developing the sensitivity of the external nervous system when it had reached the point where it was sufficient to cover the range of all ordinary incoming stimuli. As far as the invertebrates were concerned the development of the external nervous system had in a manner of speaking run ahead of the internal system, the brain. The receptive mechanism is in such animals sufficient to be able to gather a wealth of stimuli but the means of response are limited because of the comparative simplicity and fewness of the neural connections in the brain, limiting the animal to stereotyped modes of motor discharge. But the development of the internal nervous system towards greater complexity had to await the further evolution of the physical mechanism of response. The hand had to be set free from locomotion to serve as the grasping, examining, tool-using organ, and the larynx with the tongue and lips had to learn the business of speech so that behaviour became implicit as well as overt. When the hand and the eye, through the invention of writing and reading, could also act as the purveyors of thought as well as the larynx then the last great step forward was made.

But prior to this advance, which consolidated all the previous gains of individual experience and which definitely established the animal with superior cortical development as supreme, there were many preliminary steps, the consideration of which must be left to a subsequent chapter.

CHAPTER XLVII

FACILITATION

In referring to irritability as a property of living cells we distinguished three phases of this irritability in the multicellular organism. The first is the receiving of the stimulus by the sensitive surface cells, the passing on of the impulse along the conducting fibres and finally the contraction of the muscle cells, the cells which act. But because we found that animals of the same species have characteristic behaviour, or in other words, their responses are similar, we had to postulate another quality of living matter. This takes the form of an ability to retain impressions, to have the structure or composition of the nerve cell so altered by the passage of an impulse that the next time a similar situation presents itself the occurrence of the same response is in some way facilitated. In purely mental terms this process of facilitation is called memory, and it can be shown that the retention of impressions is characteristic in various degrees of all cells whether they belong in the internal or the external nervous system. We have tried to show that this retention of impressions is fundamental to the unlearned reactions of the animal and that instinctive behaviour merely follows along biological pathways, utilizing the neural trails that have already been laid down by the experience of the animal's forerunners. This process of facilitation is also fundamental to the learned behaviour of the higher animals. In the simpler organisms the purely individual reactions, if any, are entirely overshadowed by the unlearned behaviour; in man and the higher animals, instinctive behaviour is still important even though overshadowed by the learned reactions. It is perhaps worth while to reiterate that learned and unlearned reactions both rest on a mnemonic basis.

It is easy to show that memory, or impressionability plus retention, is a quality of the cells of the external nervous system but possessed in different degree according to their specialized form. The skin cells, for example, retain for a long time the effects of extreme cold even after the original stimulus has been removed. In other words they telegraph to the central nervous system the sensation of cold possibly for an hour after we have come into a place of distinctly higher temperature. What is this but the memory of the cells of the skin for cold? If our ears are suddenly assailed by a very violent concussion or series of concussions of sound we may remain deaf for some time after. More interesting still is the retention of visual impressions by the eye—the phenomena known as after-images or after-sensations. These are obtained when we look fixedly at, say, a red square for some time and then suddenly remove the square and look at a white sheet of paper. At first we have a positive after-image of a red square—another instance of a response outlasting the stimulus.

We find the same thing in the case of muscles. In a tapping experiment the muscles concerned in the downward movement need some little time to recover and carry out the reverse action. The interval of time between taps is not only due to the time that the nerve impulse takes to travel along the nerves but is also due to the retention of impressions by the muscle cells of the last stimulus. In studying the fear response of guinea pigs to a loud noise, it has been observed that there is a "refractory phase," a period of time during which, if the stimulus is repeated, the reaction does not take place. The mechanism is not set for the response. We may call the refractory phase the memory of the responsive mechanism. By some psychologists this phase is spoken of as if it were due to fatigue, but this does not seem a probable theory.

Now it is plainly apparent that if long-continued retention or memory of impressions were a characteristic of cells of the external nervous system our readiness and rapidity of response would be disadvantageously affected. It is of prime necessity for the sensitive cells of the periphery to swing back again into readiness for the next stimulus. If visual or auditory after-images were commonly

LINACRE COLLEGE LIBRARY
UNIVERSITY OF OXFORD

present for long periods our adaptability would be seriously restricted. With the differentiation of cells in the central nervous system it is possible to set aside cells whose special quality would be retention of impressions. In order for there to be a choice of responses there must be a field of choice or something to choose from. In other terms there must be some representation of past experiences in the brain and this representation can only be brought about by some more or less permanent change, which we call memory, in the nerve cells or nerve processes.

We may liken the action of the sensitive cells of the periphery to that of a swing door which will open when the impulse is given but must swing back again as quickly as possible into position. If it remained open stimuli might stream in without being in any way recorded.

On the other hand the memory of the cells of the central nervous system may be likened to the action of a swing door with a catch. If it be swung open violently enough or is opened far enough by a series of successive pushes a spring releases the catch and the door is held open.

The analogy, though it has the defect of too simple mechanics, holds good when we consider how we memorize material. Learning may be accomplished by mere repetition, which is equivalent to the opening of the door by repeated small pushes. If we depend on repetition by rote and nothing else this is an uneconomical way of learning. Spaced repetitions are better than continuous repetition. This means that we memorize best when we divide the period of study so that we go through a certain number of repetitions and then allow an interval to elapse before repeating the subject matter again. It would seem as if there were a similarity between the action of the muscle cells and the cells of the central nervous system. In muscular practice there is a warming-up period in which we steadily improve followed after a time by a decline in efficiency due to fatigue. In the same way if we continue our efforts to learn too long we do not get proportionate results from our effort. To go back to our analogy of the door—if we push it too long we may push it past the point where the spring catches and it may tend to swing shut again. On the other hand if we continue to learn until we have reached the maximum of our warming-up process and then allow an interval to elapse we are furthering not only economy of effort but also duration of impression.

But there are other ways of opening a door than by repeated small pushes; in fact, much more effective ways. Books on psychology list many ways of making the learning "push" more effective. Some speak for example of part versus whole learning, grouping of the material to be learned by finding artificial or other linkages of meaning, of the will to learn etc. We certainly do not remember things unless either we have the will to learn or a special interest in the matter presented to us. We may "get our lesson" by a confident determined attack on the subject but we also remember interesting things when this conscious effort is lacking. Retention of impressions is easiest and most effective when we recognize their relevancy to our life purposes, when in fact we take up a certain attitude towards them.

We speak of things as being striking, appealing, or interesting, meaning thereby that there is a certain tensity of feeling accompanying their presentation to us. A certain excited or mildly emotional state is an extremely favourable condition not only to the reception but also to the retention of impressions. States of excitement or emotion or rapt interest seem to involve very widespread motor responses. You have only to observe the rigidity of pose, the clenched hands, the fixed stare, the strained and intent facial appearance of the raptly attentive person to realize how widely diffused these motor accompaniments of attention really are.

The attitude of close attention has in it then something akin to that of the excitement of anticipation, where the motor reactions take the form of an inhibition of movement and a concentration of energy so that the whole body will be in readiness when the moment for action arrives. The degree of excitement will be affected by several things. Mentally there must be a realization of the extreme relevancy of the situation. On the motor side excitement seems to be dependent upon the extent of the bodily areas involved so that the digestive, circulatory, muscular and glandular systems are all affected—the emotion being greatest when we feel a thing all over so to speak. In the third place there is usually a feeling of dammed-up energy or holding back of response because of an inadequate outlet. This also serves to heighten the excitement. The sooner we can find an adequate outlet for this energy and the more channels by which it can discharge itself the sooner the excitement will be allayed. It is the feeling of limitation or inadequacy of response, and of consequent helplessness which stirs us up so completely. Indeed even though no relevant response to the situation may be possible we are often driven by this internal pressure to take some action. So we pace the floor or go through other restless motions in anticipation of some crisis that we feel inadequate to meet. The female, and the young of the human species, when faced with a situation with which they are unable to cope, may give way to crying and tears. The face is chosen as the medium of the motor manifestations of crying because it is the part of the body which is susceptible to the greatest variety of voluntary change and hence will be the best background for displaying those changes and thus making the most effective appeal to the notice and sympathy of our kind. Accordingly the mouth is set alternately in the position of vocalization and laughter, the eyes are contracted, the skin is suffused with blood, the brow is wrinkled and the tears flow, the whole combination being one of the most unusual character, combining all the facial changes carried out under stress of other emotional conditions, such as fear, rage and mirth. The fact that all the actions of the muscles of expression are combined in this way ensures that we obtain the attention of others. The effect may be eked out by loud cries and sobs, wringing of the hands, doubling up of the frame, and if the weeper be young or very feminine, may even be accompanied by a drumming of heels on the floor, or other hysterical excesses. Crying is for effect and it has usually a double one—that of calling attention to our distress and secondly of dissipating dammed-up motor energy.

Attention is a process that in lesser degree has many points of similarity to states of excitement. It is also in its motor accompaniments widely diffused so that the intense mental effort also means changes in the breathing and pulse rate, some interference with glandular and digestive functions and a muscular tension and rigidity. We are conscious of a feeling of strain or dammed-back energy when our response seems inadequate to the situation. Attention, then, seems to be in large part the act of putting ourselves into the bodily attitude which is most favourable to impressionability and retention. Movement of the body is usually inhibited when we are observing closely. Attention however differs from excitement in the absence of any pronounced feeling tone. We tend to become excited when the situation is extremely relevant from the standpoint of the furtherance or hindrance of our basic activities—when in other words there is involved in the situation escape from possible death or injury, sex gratification, the parental impulse, competition, or danger to self esteem through the loss of regard of others. These are the situations to which we attend with all our hearts, as the old saying puts it. We take up the attitude of attention and if by circumstances we are unable to make an adequate response then the dammed-up energy causes all the ensuing symptoms of excitement. Anticipatory images of the end result are not necessary to the excitement—indeed it is possible to have all the motor manifestations of excitement before the cortex can intervene, as for example, when we start with fear at a loud noise or an unexpected stimulus. On the other hand, provided there is some automatic response available, as, for example, in steering a car to avoid an accident, an emergency may be reacted to without accompanying emotional effects. However, after the situation has been disposed of and we can give the cortex the opportunity to realize the situation and to estimate its possible dangers, then an after-excitement appears. After the event we tremble and shake, the trembling being due to a mental rehearsal of the whole situation, bringing about an overflow of dammed-up energy which cannot find an appropriate path of discharge. In the same way we experience an after-glow of satisfaction over some commendable exploit which at the period of its actual happening we literally did not have time to think about.

It is fairly easy to show that states of excitement provide conditions favourable to impression and retention. An extremely terrifying experience is, as we commonly say, indelibly impressed on our minds. We can usually recall all the details of such a scene and often do, although there is a great desire to shut them out of consciousness altogether. What is this but an involuntary memory of the cells of the central nervous system? The whole of the responsive mechanism may also remember the occasion which was reacted to under conditions of intense excitement. Hence the shell-shocked soldier will sometimes retain for months the tremor which was initially set up on the battlefield as a fear reaction, or will continue the motor paralysis, the attitude of "freezing" in extreme terror, or his limbs will be set in the attitude of warding off an anticipated blow. It is to tense situations such as are met with in war that the whole neuro-muscular system, the receiving, conducting and contractile cells respond, and respond in such a way as to retain the impression—in short, the whole body remembers.

Strange to say, because of the way in which nervous energy is diffused and dissipated when we are unable to make an adequate response to a decidedly relevant situation, the attention is sometimes involuntarily directed towards some detail in the environmental background and this may receive an entirely fictitious or arbitrary importance and becomes the outstanding feature of the experience, the thing that is retained. The smell of a flower, or a snatch of melody, gives us "queer feelings" because they were once a part, perhaps only an incidental part, of some tense situation. This is probably the explanation of fetichisms, things which come to have an inordinate amount of emotional value because of the fact that they once formed part of a situation to which we responded under conditions of great excitement. At the time there was really nothing relevant to attend to, and no adequate response possible, and so in default we picked out the irrelevant detail which ever after becomes the cue for the reappearance of the emotional state.

A personal experience will serve to illustrate the way in which excitement favours impressionability or involuntary memory. The writer was being driven in an automobile at a high rate of speed along a very narrow concrete road fringed on each side by thick bushes. Suddenly a child stepped out on to the road just ahead of the car. We were travelling too fast to avoid hitting her if she had moved forward another foot, and the road was too narrow to admit of swerving to avoid her. Fortunately she drew back just in time. A moment after we flashed by a store on the plate glass window of which was printed in white letters along the arc of a circle "WAIAKEA MILL STORE." For some minutes afterwards I retained an extremely vivid after-image of these letters as if printed on the windshield of the car instead of the store window as a background. In its persistence this after-sensation resembled an hallucination. It was absent when I shut my eyes but present again when I opened them and looked again at the windshield. After several minutes the impression gradually became indistinct and finally faded away altogether. It will be noted that the situation was one to which I could make no motor response, either adequate or inadequate, since I was not driving the car. The store sign was entirely irrelevant to the situation but the fixation of the impression and its subsequent visual retention in the shape of an actual perception may have been in some way an expression or vicarious discharge of the surplus neural excitation. We may now understand why we must fixate an object for a time before we can obtain an after-image of it. In so doing we are assuming the same attitude of body that we assume involuntarily under conditions of tension but without the accompanying emotional effects. Our continued gazing at the object has the effect of deepening the impression on the cortex, or to use our former analogy it is like opening a door by means of many successive small pushes rather than by one effective push. The cells of the visual cortex remember so well that after the stimulus is removed we have an after-sensation of the stimulus. The positive after-image which may be considered as being due to the retention of the impression by the retinal cells quickly fades and is followed by the negative after-sensation in which the object retains its original form but the colours are complementary to the colour of the original stimulus. The theory most generally accepted accounts for this complementary after-sensation as a fatigue effect—the cells of the retina being "bleached" for the sensation red, the red square appearing bluish-green because we can no longer see red. The complementary colours are all that are left when red is subtracted, so to speak, from the white surface to which we transfer our gaze after fixating the red square for a period.

There are, however, certain obvious objections to such an explanation. If the cells of the retina become so readily fatigued to the red stimulus why do we not lose the ability to see red in other objects? This is certainly not the case, as we can see red just as easily if we transfer our gaze to a new object-stimulus.

There seems to be no valid objection, and certain advantages, to considering the negative after-image as being due to a cortical process rather than a peripheral. The theory which we would advance is in direct opposition to the idea of retinal fatigue. It is that the neural cells after prolonged excitation of a limited area of the visual cortex are so sensitized that they retain the impression beyond the period of actual stimulation from the retina. In other words the visual cortex is still seeing red when we transfer our gaze to the white surface. That part of the visual cortex which is concerned with the red sensation is in a refractory phase so to speak, so that the weaker stimulus—the red element in the white surface—goes unrecorded, only the bluish-green complementary colours being responded to as a stimulus. This is tantamount to an analysis of the white surface though at what neural level this analysis takes place we do not know.

This is of course a radically different theory to that previously mentioned. It would be an extraordinary thing if the retina were so susceptible to colour fatigue. This would mean that at the end of a day of picking raspberries or handling red cards we should have difficulty in seeing them. As a matter of fact practice in detecting colours has just the opposite effect. The nerve paths for the red sensation are facilitated. Similarly with regard to after-images practice enables us to obtain and hold them much more distinctly. Plausibility is lent to the theory of cortical origin of after-sensations by the fact that some people have no difficulty in obtaining them with their eyes shut.

In addition, the explanation which we give is entirely in line with what we have already said with regard to retentivity of impressions being the specially developed quality of the cells of the central nervous system. It accords also with observations regarding other types of stimuli—viz., that if a very strong stimulus be followed very quickly by a much weaker stimulus of the same nature the second will tend to be cortically unrecorded.

We may sum up the matter by saying that the positive after-image probably represents the peripheral memory of the stimulus, and the longer sustained negative after-sensation is due to the greater retentivity of the cells of the central nervous system. Both are the result of the inability of the responsive mechanism to forget what has been impressed during the period of fixed attention.

The theory of retention or memory of the cortical cells for impressions may also be useful to explain the matter of sensory adaptation, or as we prefer to regard it, cortical habituation. After a time we may fail to detect an odour that was at first apparent in a room, or we may get used to and fail to respond to the prickly sensation of flannel next to the skin, or the yellow artificial light of a room will after a time appear to be white. It would seem to be a very weak explanation to regard these familiar adaptations or habituations as phenomena of fatigue of the cells of the external nervous system, especially when we find that having become adapted to one odour or colour we can just as readily detect another. It seems much more reasonable to suppose that something analogous to the catching open of the swing door has taken place in the cortex, so that the constant instreaming stimuli of the same order having once been responded to adequately, lose their power of impressing the cortical cells which are retaining the original impression.

The cortical theory is equally applicable to the well-known phenomena of adaptation of vision to light. When we step from a dark room to an area of very bright light we are momentarily dazzled or blinded. Conversely when we step from sunlight into a darkened room at first we can see nothing, and only gradually does the power of distinguishing objects come back to us. These adaptations are usually considered to be entirely retinal. But if the cells of the retina can so easily be adapted to either strong or faint illumination why should we have such a remarkable mechanism for dilating or contracting the pupil? If the window glass can automatically adapt itself so as to restrict or increase the amount of light received why should we need window shades or blinds?

As a matter of fact the processes of adaptation to strong light and to weak illumination are surely different. The blinding effect of passing from dark to sunlight is due to the over-intensity of the stimulus and may possibly be retinal. In this case the pupil is expanded so as to be adapted to darkness and thus let in a great excess of light, the blinding effect being similar to the momentary deafness that follows a loud explosion. The sudden excitation of more than the ordinarily stimulated cortical area might also easily result in cortical inco-ordination.

In the other conditions when we pass from bright sunlight into a dark room the process is different. In this case the transition is not from a very weak stimulus to a strong but the reverse. The weak stimulus following so quickly after the strong is ineffective because the responsive mechanism is "set" for bright light. The process of habituation of vision to dim light is probably a double one—the pupillary reflex allows the exposure of a greater area of sensitive surface; and secondarily, the cortical cells take time to recover from their retention of the effects of the previous strong stimulation. The operation of the pupillary reflex is much more rapid than the whole process of habituating our vision to dim light, indicating again a cortical adaptation. To assume, as some do, that the retina automatically alters its sensitivity to fit the illumination to which it is exposed is to attribute an adaptability to one set of cells of the external nervous system that is not possessed by any other set of peripheral cells. The cells of the skin in any given area do not become more sensitive to faint tactual stimuli and obtuse to more intense stimuli, for this would be attributing discriminative appreciation to the periphery instead of the central nervous system. Instead of postulating an entirely new quality in one group of sensitive cells it would seem much more reasonable to regard after-sensations and sensory adaptations as being due to that quality of the cells of the central nervous system for which they appear to have been set aside—viz., retentivity of impressions. Visual imagery is such a well-known phenomenon that no one doubts the capacity of the cortex to call up scenes on the basis of past peripheral stimuli and in cortical disease the hallucinatory patient thinks he sees the actual objects projected in space. Hence there is no lack of analogies in mental behaviour with which to compare the after-sensation.

When a bright light is fixated for a period we get an after-image which contains areas that are constantly changing in colour during the time that the after-image is apparent. This phenomenon is referred to as a flight of colours and seems more explicable on a theory of cortical retention than on a hypothesis of fatigue of the retina. The flight of colours is probably due to the subsidence of the neural excitation in such a way as to make an imperfect synthesis of the elements entering into the colour "white."

This imperfect synthesis may be parallelled in other ways, as for example in the fading from recollection of some once-familiar scene. It does not disappear all together, but certain details are thrown into relief as it were, so that they still stand out in memory long after the general background is forgotten. It may be that the flight of colours in the after-image represents an uneven or irregular fading so that some elements are represented in cortical memory longer than others, just as in ordinary cortical memory images there will be individual differences in the retention of the elements.

To return to attention, we find that it is not true that attention is a distinctively human process. Attention is decidedly a behaviour characteristic of the lower animals, as witness the cat in front of a mouse hole. The tension of the body muscles, the switching of the tail, the fixed regard, are evidences indicating neural response to smell or other stimuli evidently resulting in dammed-up neural energy and as far as we can judge, in an accompanying feeling of excitement. This capacity for sustained attention is not by any means always associated with high intelligence. An idiot or imbecile may occupy his time with some inherently uninteresting task, such as tearing paper or twisting a string, with a fixity of attention that would be absolutely beyond the normal person's store of patience.

The ascendancy of the cortex has been established through one circumstance and that is its control of the so-called voluntary muscles. Through them it may neutralize instinctive response. It is cortical control which enables the man to walk up to the cannon's mouth although it may not prevent his knees trembling and other glandular-muscular manifestations of fear. These reactions indicate that the cortex is not in supreme command of the situation and that the lower centres are not directly under control. Many of our instinctive fear reactions, such as the nervous start in response to a loud noise, represent an over-insurance against danger, but prudence is of such importance to self-preservation that it is no wonder that our reactions in this respect are not entirely matters for deliberation and choice. As far as our fundamental needs are concerned Nature always plays safe.

When we meet with a situation and realize that it may be potentially relevant though not immediately so, as for example in the learning of some lesson or other preparatory studies, the cortex in order to ensure the deepening of the impression and its retention uses its control over the voluntary muscles to effect this purpose. It utilizes the muscular "set," the fixed gaze and all the other motor reactions which usually accompany a response to an immediately relevant situation. It puts the body into the attitude of excitement, a condition which, as we have seen, favours impressionability and retention.

The biological advantages of the emotional accompaniment are obvious. If there is a generalized or massive response, a state of tension in which all the body participates, then the animal will be alert and ready to react with its whole energy. If with this state of tension there is an added impressionability and retention, then when a similar situation recurs, there will be an already facilitated path of discharge. The feeling of excitement, reinforced by the realization that the responses which are possible may be inadequate, will be of the utmost value in causing us to seek a more adequate reaction. It is the fear of failure which causes us to be nervous, ill-at-ease or panic-stricken. The feeling of disquiet or nervous upset is of added value when it is anticipatory and in advance of the crisis whatever it may be. It is in fact like getting slightly burned before we touch the fire—a very effective protective or learning mechanism. We are thus enabled to set in motion the acts of avoidance before we are actually in danger. The cortex through its representation of past experiences is enabled by subvocal thinking to *preconstruct* a painful or dangerous situation. I may think "In ten minutes I shall be sitting in a dentist's chair having a tooth extracted" and this verbal preconstruction of the situation along with the appropriate imagery may be sufficient to bring about the anticipatory excitement of fear.

The anticipatory reaction has often a stronger emotional effect than the real experience, for when we are actually in action the attention is confined to the response and the dammed-up neural energy which was the result of the anticipation is thereby released. The setting of ourselves to a task, being "nerved up" to a situation, really means that we have a definite response in view, the neural energy directed, and this tension enables us to disregard the many perils that may beset our course of action. It is the things that we do without pausing to consider the danger that are most daringly successful. In other words a minimum of attention as regards anticipatory fear and a maximum of attention taken up with execution makes for the most effective and satisfactory response.

CHAPTER XLVIII

STIMULI AND RESPONSES

Up to this point we have described the nervous system in its simplest manifestations. We have mentioned the cells of the surface whose business it is to be sensitive to outside stimuli and to pass on impulses from these stimuli along the conducting fibres to the cells which act. At the same time we have spoken of "relevant stimuli" and the process whereby the passage of these stimuli is facilitated so that they find issue in appropriate or adequate response. But in speaking thus of behaviour we have made it so much more complicated than our description of the nervous mechanism warrants. How, for example, are the stimuli differentiated? How does the organism know which stimuli are relevant and which are not? Existence in the world is replete with countless situations all happening at once and out of these myriad happenings some are selected as having meaning for the organism and reacted to accordingly. In other terms we may say that in pursuance of its tendency towards continued activity the animal meets with certain situations which are either inimical or favourable to that continuance, and in the course of the life history of the species these organisms have learnt to react to some of these situations and so the behaviour patterns of the organism have been built up. Some psychologists have compared the animal's neural organism to a loaded gun, and the occurrence of a stimulus to the pressure on the trigger, while the explosion is analogous to the motor response. But the analogy is imperfect because the loaded gun will go off as the result of every pressure on the trigger provided it be heavy enough. But as we have mentioned, some things which are relevant to one organism's activity are entirely outside the behaviour patterns of another organism. The more complex the structure of the organism the more things or situations there are which are adequate to press the trigger, or in other words the more things there are which will further or hinder the continued life activity of the individual and should be reacted to. We may say that certain situations "call" for certain definite or set responses in the organism; but how does the organism distinguish the call from the countless other calls? Why, for example, does *Anguis fragilis* respond immediately to the sound of the pit-a-pat of raindrops and remain unstirred by all the other sounds which surround it? What new element must we interpolate in structure in order to make this differentiation possible?

If the path from sensory cell to muscle were continuous we might have a differentiation in reaction according to the strength of the stimulus. If a muscle be removed from the body it will continue, under the appropriate conditions, to respond to stimulation—strongly to a strong electric current, weakly to a weak current. Some such differentiation in behaviour we find in the simplest unicellular structures whose reaction is frequently positive to a weak, negative to a strong stimulus. But even in these simple organisms there must be some basis of differentiation between strong and weak stimuli.

Behaviour would, however, be easily explicable if it were on this simple basis of weakness and strength, but our reactions are not at all proportionate to the intensity of the stimulus. The faint buzz of a snake's rattle at our feet might be incomparably more significant to us than the clap of thunder half a mile away and our reactions are in this case rightly proportionate to the relevancy of the situation. If intensity of the stimulus were the deciding factor in determining what we should attend to then we should hear only the outspoken word and let the whisper of scandal pass unheeded. But such is not the case—it is the whisper that we want to hear. A first step towards an explanation is the recognition of the importance of the synapse, the break in the nervous chain, at the point of contact between the fibres of the affector and the effector system. We must assume that there is a certain resistance at this break to the passage of the nervous impulse, a resistance that is capable under certain conditions of being lowered so as to either permit the passage of the impulse unimpeded or to step it down, so to speak, so that it will not call forth any, or only a very weak response in the muscles. The lowering of the synaptic resistance we have called facilitation and it is probably connected with changes in both the cell body and the processes.

Borrowing an analogy from the radio apparatus we have to assume that our nervous mechanism goes through a process of attuning so that it will respond to stimuli of certain wave lengths and not to others. Moreover we must assume that the organism is born with this nervous attunement so that it responds more readily and fully to certain vitally relevant stimuli. Only by assuming some such process of hereditary attunement or biological memory can we begin to understand this matter of differentiating between stimuli as regards relevancy unless of course we postulate the existence of some mysterious "self" which stands at the switch, examines and weighs the impulses as they come in, and by opening this pathway and closing that, directs these impulses into their appropriate channels. It would be difficult also, unless we cease to rely on mechanical explanations, to understand how there could be any "stepping-up" of the impulse so that it arrives at the point of muscular discharge very much augmented and so calls forth a more vigorous or widely diffused response. We must put our explanation not on the basis of augmentation, or re-enforcement, but on the basis of diminished resistance. It is entirely consonant with this view to speak of the organism being in special readiness to act, with the synaptic resistances already lowered for the passage of certain impulses. In the lower animals this readiness or facilitation is, as we have said before, derived from the experience of all the organisms of the species that came before the individual.

But before we go further into this matter of the lowering of synaptic resistances it is necessary to look more closely at the stimulus-copula-response theory. It is very easy to show that our ordinary responses are by no means as simple and mechanical as a muscular reflex. In the latter, response is immediate, uniform and inevitable. But in ordinary behaviour there is nothing inevitable or analogous to the swing of a pendulum. Take for example the pecking reaction in a chicken. If a yellow grain of wheat is presented to a chicken it will under ordinary conditions respond with the actions of pecking. But it will only make the response if it is hungry. Why, when the chicken is well fed, does it not continue with the reactions of pecking at the grains of wheat? The answer is that part of the stimulus necessary to the pecking response comes from the animal itself. In other words the organic sensations arising in the chicken's digestive tract are represented in the animal's central nervous system. This means that the animal is in part its own environment, so that a stimulus, whether arising in the digestive or generative organs or in the muscles or in another portion of the central nervous system, can act in the same way as environmental stimuli. The organic sensations which have most to do with the self-preservative tendency are those which seem to have right of way through the nervous system and have the ability, therefore, to call forth the most diffused and generalized response. If the chicken is hungry, for example, and the grain of wheat is present, the stimulus that the food provides is re-enforced by the stimulus provided by the organic sensation of hunger proceeding from the cells of the digestive tract. The organic sensation of hunger is one of the situations or stimuli to which it has paid all animals of the species to respond to immediately. If the food is not present the response of pecking would be inappropriate, so the neural excitation is diffused and the animal goes through the movements of walking, scratching, etc., movements in short that in the past experience of the species have brought the animals within reach and sight of food. When the organic sensation disappears the appearance of the grain of wheat is insufficient stimulus to call forth the response.

The advantage of a diffused response is shown by another instance cited by Kohler. It is part of the unlearned reactions of a young child or a monkey to follow with the eyes the movements of a light. A monkey was operated upon and the muscles which ordinarily give, say, a right to left movement of the eye-ball were dissected out and reattached in such a way as to give the opposite movement.

After recovery from the operation the bandages were removed and the light was shown, the assumption being that if the nerve impulse followed its usual path the monkey would perforce turn his eyes in the opposite direction to which the light was moved. However, the appropriate light-following reaction even though carried out by the opposite action of the muscles resulted immediately. The response called for by the moving light was the following movement of the eyes and this came about by whatever mechanism was available. When the already facilitated nerve path did not bring about the appropriate result the nervous excitation continued until the path of appropriate discharge was found, just as in the same way the activity of the chicken continued until the expenditure of the diffused impulses brought about the situation in which an adequate response was possible. Thereafter in the case of the eye movement the new pathway became the facilitated one. Additional evidence on this point is provided by other surgical operations. In cases where the musculo-spiral nerve which innervates the muscles which carry out extension of the wrist and hand has been severed, the muscles which ordinarily act as flexors are brought round and re-inserted so that they can now act as extensors, with, of course, their original innervation through the median nerve (see Chapter III). When after recovery from the operation the command is given to the patient to extend the hand, he carries out the movements of extension, slowly and with difficulty it is true, but correctly, and this by the agency of the muscles whose previous business was flexion. What has happened? Evidently the nervous impulse took its already facilitated path down the musculo-spiral nerve to the point of severance but was unable to discharge itself there. We must assume, then, that a counter current through the afferent fibres accompanying the motor nerve was set up to the motor area of the cortex, and that the neural energy there became diffused until a path was found by which it could be discharged by way of the response that was adequate to the situation. The first reaction is weak and uncertain because of the draining off of energy through diffusion, but immediately the appropriate response was made the median nerve became the facilitated pathway, and the action of extension came to be performed thereafter with more and more certainty and despatch. Neurologically, the process consists of the bringing to one point of discharge the diffused neural energy and the inhibition of other unnecessary muscular reactions.

It is probable that the specific or adequate reaction represents a selection from among the generalized or diffused paths of discharge and that the diffused reaction represents the primitive response upon which we fall back if the means of making an appropriate response are absent. It is in the nature of a trial and error operation within the nervous system of the organism itself.

It is interesting to observe what class of stimuli call forth this diffused or generalized response, or as we might say, those which have the open road, the right of way through the nervous system. Take for example the effect it has on us if someone, no matter how familiar, jumps out suddenly from behind a curtain and says "Boo!" There follows a widely diffused response. No matter what we may be intent upon, the whole stage is usurped by this new stimulus. We give the gasp of fear, we feel the quickened breath, the sudden acceleration of the heart beat, the convulsive start and the temporary but real feeling of excitement. This generalized reaction has already been explained as being useful in the way of bringing about a general alertness or waking up of all our physical forces in readiness for action. To some degree, however, the body is not in readiness for appropriate action and indeed the first movements may be somewhat irrelevant as regards escape. In such an event, the person is popularly described as having "lost his presence of mind," but as a matter of fact, his cortex was not engaged in the matter at all. It would seem as if the main value lay in the excitement itself, the increased impressionability of the nerve cells so that the situation itself will be remembered. It should be noted also that the reactions seem entirely involuntary and take place before there is any discriminative element possible. Our reactions are just as violent if it is our most intimate friend who thus startles us, as they would be if it was a burglar or an assassin intending to do us grievous bodily harm.

There are several factors in the situation which must be present to call forth the most complete fear reaction. In the first place the appearance must be entirely unexpected. If we know that someone is in hiding it is easy to inhibit the manifestations of fear. The second factor in the situation is the imminency of the object, which must be within reaching distance as it were. We are not at all excited if our friend steps out, no matter how unexpectedly, from some point of concealment a hundred yards away. Further, our alarm is in a certain degree proportionate to the size of the object. A small child suddenly appearing does not occasion the same start of fear, and in such cases the nervous reaction seems to have a discriminative basis, a fear of injuring the child by bumping into it rather than any fear for ourselves. It may be, however, that size of object is of importance only in so far as it is interpreted in terms of imminence. The two primary factors seem to be, then, unexpectedness and imminence of the object.

As regards auditory stimuli there must be present the factors of unexpectedness and intensity although intensity may also be sub-cortically interpreted in terms of imminency. A toy pistol shot off behind our ear may occasion a more complete fear response than a cannon fired a mile away. The touch sensations which call forth the fear reaction must also possess the quality of unexpectedness. Intensity does not seem to be of the same importance, as for example our initial reaction to the prick of a pin may be just as complete as to a stab from a dagger. When the appeal is to protopathic sensitivity the reaction is more readily called forth than it is to epicritic sensations. Grasping or seizing, if unexpected, will give us a greater start than mere touching or light contact, and since all contact involves imminency of the object responded to, unexpectedness is here the only factor involved.

Other occurrences to which we respond with these widely diffused reactions are sudden slips or withdrawals of support. These are among our most primitive reactions as they are the most easily called forth in the newly born child; the loud unexpected noise is also one of the situations which call forth the primitive fear response in the child. In these primitive fear reactions our behaviour is certainly not far above the level of that of the amoeba when it is pricked with a drawn glass point. The response seems certainly free from all cortical control since we start first and recognize the person startling us afterwards. It would be interesting indeed to observe the fear reactions under these conditions of a case of cortical paralysis or hemiplegia. It would be possible then to prove whether the emotion of fear or the muscular response was the primary factor. In all probability the centre for initiating the start of surprise is not cortical but at a lower, striate level. The reason why imminency is an important factor is apparent when we consider that the sensations involving actual touch or contact are naturally those to which the animal must learn first to react. As regards stimuli coming from a distance, in between the perception and the ensuing response there is time for deliberation, possibly for anticipatory motor movements as in the quivering of muscles prior to the spring or leap, and in the human being for vocal or sub-vocalized thought as a rehearsal of the motor response. The anticipatory cortical rehearsal is most important as we can foresee or imagine the situation, project ourselves into it, and prepare a course of action. Hence as a prerequisite to the ability for planning, forethought, choice of response, and the experimental procedure, we must have the development of distant sense receptors such as the eye and the ear. This is such an important consideration that we shall return to it later. For the present we should take note of the fact that while the animal was limited to touch and a chemical food sense operating at a very short distance its reactions had to be so immediate that hardly any delayed choice was possible.

How hard it is for us to unlearn this primitive behaviour is realized when under stress of great fear we revert to the trembling of the limbs which in the animal may have been useful as the anticipatory movement of flight, whereas in the human being flight is by no means always the most adequate response. Our sudden paralysis in terror may also be analogous to the "freezing" of the animal in its "form" or lair. We may even copy the animal in having our hair stand on end which may have been useful to the animal in increasing its apparent size and formidability.

It is noteworthy that both in the lower animal and in man "freezing" or the paralysis of fear only takes place when the animal or person is at the time of the terrifying appearance already immobile. Apparently if the animal is in motion some of the fear impulses are dissipated through the continuance of the muscular reactions.

In summarizing this discussion we may say that our neuro-muscular organism is pre-organized for response to certain situations involving the sudden and unexpected appearance of a large or imminent object and these situations provide what may be called prepotent stimuli—stimuli, that is to say, which have right of way over our neural pathways and which call forth diffused reactions. It is probable that these reactions are the most primitive and from them have been selected the pathways of specific response. If for any reason these pathways are blocked or if the usual definite response seems inadequate then we fall back on the more primitive reaction.

It is obvious that in the organism which has a very simple central nervous system most if not all of the pathways would be concerned with the instinctive or unlearned reactions. In such cases, given a stimulus of sufficient strength, the impulse will travel along the predetermined or most available pathway and a stereotyped response will ensue. An example of this direct, immediate, inevitable response is the pupillary reaction to light. But in order to deal with new situations or even to bring about differentiated action there must be added complexity of the nerve connections and new synaptic resistances to be overcome. By adding to the complexity of the nerve connections a certain immediacy or directness of reaction had to be sacrificed.

We may now return to our original question—how does the stimulus gain this prepotency? It is easy to see it is not a matter only of intensity. The fish, for example, may respond just as violently to a sudden prick in its side as it would if it were jerked completely out of water. The explanation seems to be that these unlearned reactions are really lower level responses; or it may be that they are so primitive that they flow along already facilitated pathways in the cortex, pathways so deeply grooved that the impulse when it arrives at the end plates of the motor nerves does so with such undiminished force that it sets up a relatively powerful muscular reaction. The rôle of the higher centres seems to be that of inhibition and the very fact that unexpectedness is the dominant factor in these mass reactions of fear would seem to show that the cortex is not involved. When the distant sense receptors are able to play their part and give warning to the cortex or when the cortex is otherwise prepared for the sudden appearance then we do not have the start of fear. It is probably quite wrong to speak of the direct control of the lower nerve centres by the upper. What the cortex controls is the voluntary muscles. This is shown by the fact that we only partially inhibit some of the reflexes and others not at all. By tensing the muscles of the leg we can partially control the patellar reflex. If, however, the cortex is given the task of initiating another set of voluntary muscular reactions such as those involved in pulling on the interlaced fingers then the knee jerk can be elicited much more perfectly. This is sometimes called a process of facilitation or re-enforcement. It is, however, merely the removal of inhibition and allowing the knee jerk a clear field. Where there are no sets of muscles under voluntary control to counteract the reflex action as in the pupillary reaction to light, then the response is inevitable. How complete is this inhibitory control of the voluntary muscles by the cortex is shown by the free play of the lower motor neurons when the influence of the cortex is cut off. When the influence of the cortex has been removed by severance of the spinal cord stimulation of the glans penis will bring about the movements of coitus. The most effective victory over the urgings of the appetite is achieved when we literally run away from temptation or in other words provide an actual outlet for the neural pressure.

Some such theory of lower response, free from cortical inhibition, seems to be necessary to account for the altogether disproportionate response to exactly the same stimulus when expected and unexpected. Even the strongest man cannot resist the nervous start if suddenly pricked by a needle—especially if the attack comes from behind. Because we have no eyes in the backs of our heads we are extremely vulnerable to surprise from that quarter, so that the very act of turning one's back to one's foe increases the fear reaction. When we are naturally in an excited or nervous state the number of stimuli which find an open right of way through the lower nerve centres to the muscles seems to be greatly increased. We may at such times start at shadows, or the slamming of a door, or almost any unexpected sight or sound will frighten us.

Some stimuli such as those that involve painful contact of some kind find such facilitated motor pathways that the ordinary muscular reactions are insufficient to adequately discharge the nervous energy. It is as if the ordinary channels of discharge were too limited to relieve the neural pressure and consequently motor reactions continue long after the disappearance of the original stimulus. Evidently something analogous to what happens with a severed nerve takes place—a counter current is set up, returning to the nerve centres in the brain, keeping them in a state of excitation and thus continuing the motor reaction long after the need for it has ceased. The dog which has had a tin can tied to his tail will keep on running long after the can drops off. This does not mean that the dog continues to have mental imagery of the embarrassing situation but merely that a great deal more neural excitation has been produced than can be discharged at once. Hence the dog continues to run until the excitement subsides. It may be that the neural counter current from the motor end plates back to the synapses may help to explain the process by which permanent or biological facilitation takes place. It may also assist us to understand a process of what we might call over-facilitation in learning a "catchy" melody or jingle, one that is, whose rhythm lends itself to ready repetition. The rhyme or tune is one that we hear repeated over and over by someone else but which at first we learn with some difficulty. This effort to remember, plus the constant motor repetition, causes a reciprocal neural excitation. Thereafter the response seems to pass beyond cortical control. Any rhythmical sound such as the clicking of the cars over the railway track joints, or running water, is enough to form a stimulus which flows along the over-facilitated path. Even in default of any outside stimulus we find ourselves repeating the tune over and over again, until we ourselves are quite sick and tired of the performance. Here again we have an instance of a response persisting long after the original stimulus has passed which seems best explained by the theory of cerebral counter-excitation. In this sense it resembles a visual after-image which, as we have stated, probably results through over-excitation of one area of the visual cortex.

In the case of conditioned fears there is a keying up of the senses, an attuning of them to a condition of receptivity, so that they will be on guard against surprise. The man who has lived in snake-infested country knows the feeling of alertness which never seems to be relaxed. His eyes rove over the ground and he will start at the sight of a shadow or a stick or a piece of rope in the grass. This watchfulness will persist even when he has been long absent from a country where snakes are found. Possibly this prolonging of wariness beyond the point of necessity is due to a counter-current along the sensory pathways from the temporarily excited brain centres to the periphery, and is analogous on the motor side to the singing over of a tune long after we wish to forget it. The stimulus in this case is the walking over ground similar to that in which snakes are usually found. The appearance of the ground formed part of the original stimulus pattern. The writer after living six years in a country free from snakes is occasionally conscious of a watchfulness the direct stimulus for which has long been absent. This increased watchfulness is evidently quite involuntary. The mother will wake from the deepest slumber at the slightest cry of her infant in the night while remaining oblivious of many louder sounds. The cry of the infant is not of course a more intensive stimulus than other sounds, but it finds an already pre-sensitized sensory mechanism and an already facilitated path of discharge.

The theory of neural counter-currents, hypothetical as it may be, would help to explain how the cortex is able to give a stimulus voluntarily attended to as much weight as a biologically prepotent stimulus. The cortex can give depth of impression to the situation by its control of the voluntary muscles. It can make all the senses stand at attention so to speak and at the same time give to the muscles all the tenseness and rigidity of response. This will be effective in setting up neural counter-currents which will add to the excitation of the neural centres involved in the specific behaviour pattern. In other terms we may say that the sight of a snake calls forth the same response as any instinctive fear because in the first place we have trained our senses to look for snakes and at the same time have held our muscles in anticipatory tension ready for a response. There is thus a readiness to see and a readiness to act. The constant anticipatory attitude and excitation without adequate discharge has the effect of setting up counter-currents and thus augmenting the central neural excitement. Indeed always to look for snakes but rarely to see them is worse than seeing them every day, since in the latter circumstances the taking of the appropriate action discharges the neural excitement; we get used to the situation. When we are alone in a house at night we may get into a state of nervous excitement in which we find ourselves listening for every sound and at the same time holding ourselves in a position of physical strain as if anticipating flight. The requirements for the allaying of unnecessary fears are first of all the relaxing of the sensory vigilance and secondly of the muscular tension. With these two conditions removed, the central neural excitement will abate and the synaptic resistance be built up again to its normal level. We shall then cease to start at shadows and to jump at insignificant sounds. In certain conditions of high nervous tension due to overwork or ill health our nerve pathways are so over-facilitated that every unexpected occurrence, no matter how slight or simple, jars us tremendously.

In dismissing this matter of the right of way that the prepotent stimulus has over the neural organization one might ask why it is that the cortex has not assumed dominion over these lower level reactions. Many of these diffused reactions are uneconomical and from the standpoint of common sense seem foolish and unnecessary. Why should a sudden slip cause us such nervous upset if cortical control would obviate this effect? We have already said that the increase in complexity of the neural connections causes us a loss of immediacy of response. It makes choice of reaction possible but creates also the possibility of a wrong choice. The instinctive response may err but if it does it errs on the safe side. The reaction is sometimes more than adequate, and in that sense unnecessary, but it is rarely inadequate. The start of fear is due to the potential threat, and is already consummated before we can decide whether there is real danger in the situation or not. It is worth while to reiterate that Nature in as far as she plans our behaviour along instinctive lines always plays safe.

This brings us to a very interesting conclusion. It was certainly not worth Nature's while to endow us with an organ of delayed choice until she had already provided us with the distant sense receptors that will make that delayed choice safe. Deliberation under certain circumstances would be an extremely dangerous thing for the organism to indulge in. Certain stimuli are reacted to through the lower level centres because they possess such a quality of imminency that the cortex has no time to choose a response. When you are pricked unawares with a pin the cortex cannot do anything towards avoiding the painful stimulus. On the other hand the detection by the distant receptors of an approaching danger will give the cortex time to deliberate and respond adequately. From the standpoint of self preservation the most highly developed cortex would surely be of no value whatever to a man who was robbed suddenly of sight and hearing; he might as well be decerebrate. In other words, if he can only exercise his power of choice when things actually touch him, he may as well be without the power of choice. The survival of such a person is of course entirely dependent upon the extent to which he can borrow the distant sense receptors of other people. One would not, therefore, naturally expect a highly developed cortex in an animal whose self preservation depended mainly on the sense of smell, which is not a very reliable distant stimulus receptor. It is not to be wondered at, then, that the area of the central nervous system that subserved this sense—the smell brain—should be diminished to make room for the higher development of the pallium.

CHAPTER XLIX

BUILT-IN HABITS

One of the troubles of this over-instructed but ill-educated generation is that its vocabulary is too large; literally it knows too many words. There is a tendency in us to hit upon a word for some wonderful process in nature and in so doing to imagine either that we and other people know all about it or that we are absolved from any further thinking about its high mystery. Language in such case becomes not so much the art of concealing thought but rather the art of concealing the absence of thinking. The discussion of well-instructed people is very often a bandying of high-sounding words—words which owe their power, like the kings of old, to some divine right, and are not subject to the ordinary necessities of justifying their existence through being definable in terms of common meaning. Such words are extremely convenient for covering over those wide gaps that exist in our understanding of commonly observed phenomena. One of these words is instinct and while it is a perfectly good word we should not delude ourselves into thinking that we need not trouble our heads to explain or to try to understand the phenomenon so conveniently named and disposed of. On the other hand it is quite worth while to stop and consider how wonderful is this matter of the handing on from generation to generation of the learned reactions of the race which are the unlearned reactions of the individual.

Our wonder is immeasurably heightened when we discover how remarkably complicated most of these unlearned reactions really are. Take for example the apparently simple movements of flexing and extending the hand and fingers—movements that are within the capacity of the new-born babe. These movements have been described in detail in Chapter XXX, at least to the extent of the part played in them by one not very important muscle. We have seen that this muscle acts in six different ways and in so doing may play the parts of agonist, antagonist, synergic and fixator in turn. Then too the action of the muscle itself in any one of these movements may be a fibre by fibre affair according to the extent or the power of the movement. Other muscles may also be called in to assist in various ways so that the whole consists of a most wonderfully complicated series of actions. When we stop to consider that our movements consist of very many combinations of such sequences and that the body itself is a most intricate bundle of such mechanisms, then we begin to see the reason for that remarkably complex arrangement of nerve connections of which Herrick speaks. As we pointed out in Chapter XLV, our unlearned behaviour patterns are truly marvels of muscular nervous co-ordination. Yet the ordinary text-book in psychology speaks of a muscular reflex as if it were mechanically as simple as the raising of a weight by a string passing over a pulley. As a matter of fact nothing remotely approaching this mechanical simplicity exists in the human body but each reaction appears as the end product of a wonderfully balanced and complex-hidden mechanism, the parts of which act in definite sequence and degree. It is worth while to repeat that our unlearned motor reactions certainly did not come about originally as perfected ready-made stereotyped sequences. They were surely the product of an interminably slow process of gradually increasing perfection, Nature taking advantage of every slight variation in individual structure first to build up and finally stamp in every advantageous addition to neuro-muscular habits. In this connection it is hard to believe that variations in individual capacity and experience did not play their part in building up the inherited pattern of behaviour, although it is true that as regards the transmission of acquired characteristics experimenters have not so far been able to demonstrate, beyond peradventure, such transmission under rigidly controlled conditions.

However, though the means and methods may be in doubt, the fact is certain that reactions are certainly "built-in" together into series so that each one in its order serves as a cue for the appearance of the next response, the whole being bound together in the same way as the notes of melody follow each other to make a tune. Bearing in mind the danger of the misleading simplicity of the analogy we may liken unlearned reactions to the music rolls of a mechanical piano player. Biological memory stamps in the impressions on the central nervous system and these are translated into the movements of the single keys (or muscles) which in turn have their issue in the completed action or melody.

The way in which actions are linked up in series, the nature of each being affected by its place in the series and subject to the influence of the action which comes before it, can be illustrated by the electrical stimulation of the surface of the brain in the motor or pre-central area. In one experiment stimulation of successive points in order from above downwards resulted at a certain point in flexion of the elbow and thereafter in movements of other parts. When, however, the stimulation was in the reverse direction, from below upwards, the point which formerly controlled elbow flexion now produced movements of the thumb, and it was not until a point much higher up was stimulated that elbow movements were again elicited. Evidently the reaction was determined in large part by the action which took place immediately before it. This shows that there is a constant tendency for muscular reactions not to remain isolated, but to group themselves in appropriate action patterns or series, the occurrence of one movement paving the way for the appearance of the next. In playing new melodies of movement Nature evidently prefers to use chords rather than single notes.

In considering instinctive behaviour we are often puzzled to account for the building up of the pattern because frequently we find actions interpolated in the series for which we are entirely at a loss to account, especially when some of these unlearned reactions do not seem to have any bearing as regards the biological advantage of the animal concerned. Such for example are many activities which have for their apparent purpose the preservation of the race. It would seem as if the basic tendency which we postulated as characteristic of the behaviour of living matter—viz., the tendency to seek that which furthers, and to avoid and resist that which hinders its continued life activity—would surely need to be supplemented by a race-preservative instinct. This is indeed the almost universal viewpoint. But how did such a tendency come to be fixed as part of animal behaviour? It is, as we have seen, not a part of the original life equipment of the unicellular organism. The evolutionary hypothesis seems to be most firmly based on the idea of changes of structure leading to adaptations of function which are in some way advantageous to the animal concerned, and a corresponding disappearance of those that are no longer of use or value to the animal. But so many of the actions of animals in connection with the care of their young are apparently divorced entirely from any element of individual or self advantage. It would seem as if the so-called race-preservative instinct rested entirely on an altruistic basis absent entirely from the rest of the animal's behaviour, and was therefore one to which the evolutionary theory does not apply.

For the better understanding of the problems involved it might be well to summarize briefly the theory of the origin of the reproductive habit set forth in Chapter XLIV. We showed that reproduction by fission might quite conceivably be interpreted as being of biological advantage to the reproducing animal. It was tantamount to the division of life-capital and its reinvestment in new organisms, thereby increasing the chances of survival of some of the subdivided portions. We also showed that originally over-production or mere multiplicity of numbers was of advantage to organisms that had no means of offence or defence against their natural enemies. In such conditions reproduction was of decided potential value to the original organism. There may be, in addition, conditions of polarity in the cell itself which render its division necessary or advantageous. Once reproduction became established as part of the life cycle of the unicellular organism then it may be considered as derived originally from the basic self-preservative tendency instead of being regarded as part of the original life equipment of the cell. The importance of reproduction to the survival of the species was such that it dwarfed into insignificance its original value to the individual. Naturally only the amoebae that were the product of amoebae who had incorporated fission into their life cycle had the chance of continued survival, and so reproduction came to be almost as important an activity as the self-preservative tendency from which it was derived. In the process of development many of the acts of the reproductive cycle became more and more specialized with regard to race preservation so that their original value from the standpoint of self advantage has been quite obscured.

In the more highly developed animal, as we have seen, reproduction became the business of a special set of cells, but it still remained a process of fission, a division of the new germ cell from the parent individual. On account of the advantage that mixture of protoplasmic strains conferred, bi-sexuality was developed and finally the conflict between the active male and the passive female rôles in generation brought about hetero-sexuality—a condition which became invariable in the higher animals but did not develop generally in plants because they were not mobile, the differences in the sexual rôles being insignificant in vegetative organisms, in which the pollen and not the organism itself travels.

In the animal which has developed special organs for reproduction the biological importance of the function is such that sex craving comes to be one of the strongest drives towards action, taking second place only to hunger, fear, and pain, organic sensations fundamental to the self-preservative tendency. Experiments have shown that even in female animals of infrahuman status the sex drive may at intervals equal that of the male. A recurring oestrous period is Nature's way of striking a balance between constant sex activity on the one hand and constant passivity on the other. Periodicity of desire lacks the stultifying effect of passivity while retaining some of its conservative effects. In many cases sexual periodicity is of advantage to both parent and offspring when it synchronizes with the season of food abundance. In races of man living in parts where there is a distinct difference of seasonal food supply conditions, this periodicity is more apparent.

But granting all this, there are still some very puzzling problems to be faced when we consider the reproductive habits of some animals, for there seems to be no lack of instances of actions performed apparently solely for the advantage of the young and not for the animal itself. Such for example are many of the activities which have as their most apparent purpose a provision for the young in advance of their birth. The animal in such cases has no foreknowledge of what is to happen, yet invariably, according to its species, it performs whole sequences of acts which are apparently meaningless except in relation to the future event. We have a common example of this in the nest building and incubation habits of the bird, a whole sequence of anticipatory actions having no reference apparently to the welfare of the bird itself but which finds an inevitable place in its reproductive cycle. It would seem almost necessary to refer these acts to a special race-preservative instinct. But even if we invoke such an explanation it still seems difficult to account for the interpolation of such an activity as nest building in the reproductive series. In a chain of reflexes such as is involved in a limb movement we find the whole sequence of muscular actions appropriately linked together each serving to call into action the action succeeding it, and having reference to the one final result, the accomplishment of the completed movement. If the chicken is hungry the sensation serves as the relevant stimulus for the muscular movements which bring it in sight of the grain of wheat and the pecking response inevitably follows. But in the reproductive cycle of birds it is difficult indeed to understand how mating and fertilization can serve as the relevant stimulus for such an activity as nest building. If the hungry bird stays inactive it will remain hungry and there will be no further result of the stimulus, but in the case of the reproductive sequence once fertilization has occurred the eggs will be laid whether a nest is built or not. The nest building activity is apparently unrelated to the acts in the series which come before it but is entirely meaningful in relation to the incubation of the eggs, an activity which comes after it in the series. It would be easy to understand if the nest building began in response to the presence of the eggs but as it is, it seems as if the adequate response preceded the relevant stimulus.

In still higher animals such as the mammals there are often similar, if less elaborate preparations for an event of which the animal can have no foreknowledge. The rabbit, for example, prior to giving birth to young, digs a short burrow apart altogether from the general warren and lines its inner chamber with fur, sealing the mouth of this burrow every day with well-stamped earth and opening it at night. These preparations will anticipate the birth of the young by some days and the burrow is kept sealed by day until the young are capable of a measure of self protection. This habit of the female rabbit has the effect not only of protecting her offspring from predatory animals but also from the male rabbits who will readily attack and kill them. It is difficult again to explain these activities without calling in a race-preservative instinct and still more difficult to explain how fertilization or approaching parturition should serve as cues for the nest building. How did these discrete activities come to be linked together in the one behaviour pattern?

But in considering the evident value of the particular reaction to the young we may lose sight of the fact that the activity in question might originally have been of value to the parturient animal itself. Not all birds build nests—many of them choose the hollows of trees. Judging by the time it takes a bird to lay an egg the business is a somewhat long and certainly a laborious affair. It is obvious that at this time the bird being perforce immobilized, and in no condition for flight or defence, some means of concealment would be decidedly advantageous. But hollows in trees are not very numerous and may be pre-empted by the larger species so that the bird who found a space in a tussock of grass or who learned to interlace a few twigs as a concealment for herself and a convenient repository for her eggs was conferring an undoubted advantage on the unborn young. The nest building habit thus becomes established as an inherent unlearned reaction because every bird who had previously used a concealment device had increased the survival chances of herself and her young. Whatever physiological or structural dispositions were the basis of the habit were evidently transmissible by inheritance. Finally the self-protective character of the activity became dwarfed into insignificance, in comparison with its importance to the survival of the young and so it became incorporated into the reproductive cycle as a racially conditioned reflex. The process may be illustrated diagrammatically as in Figure 77. This shows how nest building which originally was a self-preservative tendency became interpolated within the reproductive sequence. Since nest building comes naturally before egg laying it came to be associated with the physiological changes consequent on fertilization so that these or fertilization itself became, by the process of conditioning, the cue for the nest building activity to appear. Since its value to the offspring far outweighed any self-preservative value it ultimately became a part of the reproductive sequence or pattern of behaviour.

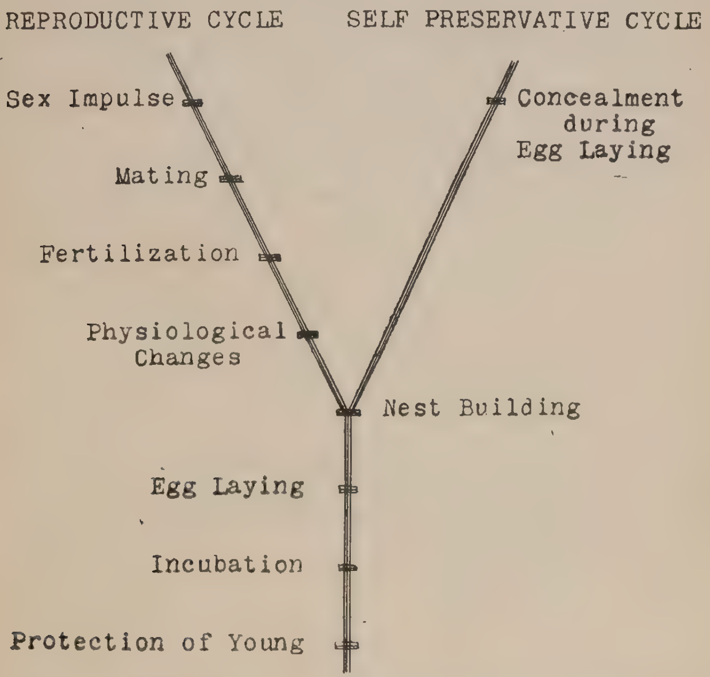

REPRODUCTIVE CYCLE
SELF PRESERVATIVE CYCLE
Sex Impulse
Mating
Fertilization
Physiological Changes
Concealment during Egg Laying
Nest Building
Egg Laying
Incubation
Protection of Young

FIGURE 77.—Indicating the manner in which a self-protective mechanism may be incorporated into the race-preservative sequence of acts. Nest building has lost its original meaning as a self-protective device.

The habit of brooding or incubation is another illustration of the manner in which a reaction of minor value to the parent will tend to become fixed because of the advantage it confers on the offspring. We are all familiar with the change of physiological disposition that occurs in the domestic hen at such times. From being an easily disturbed and frightened bird it develops unwonted pugnacity and obstinacy so that actual violence is often needed to get it away from its nest. This change in disposition evidently has a physiological basis and if it continues after the incubation of the eggs its advantages to the chicks are obvious. We may say then, that all the young whose parents develop a pugnacious habit synchronizing with the period of their helplessness will have a greatly increased chance of survival.

It might be objected, however, that whilst changes in the physiological disposition consequent on egg laying might serve to explain the incubation habits of the hen bird it would not account for those instances where the male assumes the business of brooding and incubating the eggs. This behaviour is characteristic of the Ratitae to which sub-class the ostrich, the emu, and the rhea as well as the less common kiwi and cassowary belong. The ostrich may be taken as an example of the breeding habits of the rest of this sub-class. He is polygamous and his four or five hens lay their eggs in a communal nest or hollow, very carefully concealed. After ten or a dozen eggs are laid the cock bird broods and sits at night on the eggs, the duty of guarding them by day devolving on the hens in turn. At first sight such behaviour seems unaccountable, except on the basis of some specialized instinct. It must be remembered, however, that these are plains-dwelling birds and of the largest size. Being flightless they are compelled to roam over large areas in search of food and water so that as a consequence a communal system of incubating the eggs and rearing the young is advantageous. It may well be that in a polygamous bird there are changes in the reproductive system of the male that makes the sitting on the warm eggs at night a source of satisfaction to the bird. Obviously there would be trouble if the brooding impulse were strongly present in the females as in a communal nest only one bird can sit at a time or the eggs would be broken. Again, the advantage to the offspring of the male bird's habit is so obvious that its original meaning has become insignificant in comparison. As regards another class of birds, the Passeres, in some of which also the male bird incubates the eggs, there are very striking structural changes associated with the breeding season so that the warmth of the nest might easily serve as the stimulus for the incubating process. Whether this explanation of the male bird's habit be the true one or whether some other be found, it does not seem necessary for us to fall back on a "paternal instinct" as the original motive for this behaviour.

The protection and feeding of the young is of course an activity on a different footing. There the presence of the young themselves may provide a relevant stimulus for the protective action. Possibly mere familiar association may serve to call it forth, as may be illustrated by the behaviour of animals which have adopted others of another species and to whom they give care and protection. Even in the feeding of the young by the parents there may be a self-protective element since their cries may easily serve as an advertisement of their presence and thus attract the attention of their natural enemies, and increase the danger to all. This also applies to the helpless and wounded which are sometimes succoured by the rest of the herd or group, and sometimes killed. In all probability the action did not have its original basis in any altruistic concern for the distressed for it has in it also some element of the self-preservative tendency.

The fact that in birds and mammals the so-called race-preservative instinct varies so much would seem to indicate that it is the result of a complex of factors. Some birds build their nests, others do not. The hen birds may do all the incubating, part of it, or none. The young may receive care for a long period or they may be almost self sufficient shortly after hatching. The same variability of behaviour is exhibited by mammals. In some cases the males will assist in the care and protection of the young, in others they are likely to attack and devour their offspring. Under specially disturbing conditions such as those which captivity usually implies, the females will also kill their young.

The race-preservative instinct, if such it is, seems to be a remarkably uncertain and variable affair.

Generally speaking, though there are many examples of animal behaviour for which an explanation in terms of biological advantage is not readily available, the building up of the unlearned reactions of the type we have been considering would be much less mysterious if we regarded race-preservative tendencies as being offshoots of the basic tendency of self preservation. Such a theory would naturally make a difference in our interpretation of many acts. Instead of regarding the habit of the cow in seeking concealment prior to parturition as indicating anticipatory provision for the calf, it should be thought of as originally an impulse which favours her own protection, during temporary helplessness, against her natural enemies or those of her own kind. By racial conditioning the sensations preceding parturition have become the cue for the habit to appear.

In relating the race-preservative to the self-preservative impulse we are not blind to the fact that much of animal behaviour, especially in the lower forms of life, seems inexplicable. But we must remember that once reproductive habits became established as part of the life cycle they were of such overpowering importance as to capture, so to speak, many of the acts which originally had a self-preservative purport. In this way the habit of certain wasps in building mud nests and filling them with the bodies of other insects so that the newly hatched larvae may have food, may have been originally a mere food-preserving device which has had its character changed completely by being incorporated into the reproductive cycle.

To many people this may seem a novel idea. Hitherto in thinking of the evolutionary process they have fixed their attention on those variations in structure and consequent behaviour that are advantageous to the animal in adjustment to its environment, neglecting the fact that habits of the animal may have a far greater significance as regards the survival of their offspring. Others may object to any theory that implies inheritance of individual habits, or their "building-in" as racial characteristics. But whatever may have been the methods of this building-in process the fact itself seems certain. The absolute interdependence of structure and function and their common relation to environmental influences is shown by the similarity of habits of birds of similar structure such as the rhea, ostrich and emu. As we have pointed out, these birds are large and therefore they are flightless; they dwell on plains where food is scarce and therefore they become communal in their nesting habits. With the communal custom established the male assumes the responsibility of incubation. As to the structural or physiological conditions which provide the immediate stimulus for these actions we can only conjecture. Complex as these behaviour sequences may be, they are, we must remember, simple in comparison to the inbuilt habits of muscular action which are exemplified a hundredfold in our own bodies. True it is that many of us strain at the evolutionary gnat and swallow the camel. There is an older school of thought which explained all instinctive behaviour of birds and mammals as being due to an instant and continuous direction by a mysterious providence—a divine power which kept its finger eternally on every animal mechanism, steering it in the direction of its own good, or worse still, of ours. "Purpose" fell into scientific disrepute because the word implied this simple view. But this school of thinkers was surely not so far behind that of a later day which labelled everything it did not understand as an "instinct" without feeling any necessity to explain from whence the instinctive behaviour was derived. Apparently it was plucked by the animal from the air. It is of course impossible to find for all animal behaviour a ready explanation in terms of individual biological advantage but to assume that the race-preservative tendency is entirely altruistic in origin is little better than to ascribe it to some extraneous and untrammelled design. On the other hand, while fortuitous changes in structure leading to the formation of habits in the parent of ultimate value to the offspring have undoubtedly played some part in the building up of the reproductive sequence of acts, these do not account adequately for the origin of the race-preservative tendency itself

CHAPTER L

PREPARING FOR THE CORTEX

The development and functioning of the cortex was, as we have seen, the culminating point of a long line of advances in neural structure. In the first place it entailed the setting aside of cells whose special quality was the more or less permanent retention of the effects of stimuli and responses. For the cells of the sensitive surface and of the muscles this condition of permanent impressionability was of no advantage, a quick swing back to equilibrium—a forgetfulness—being essential to their best functioning. The cells of the cortex became the mechanism of choice of reactions, and retentiveness or memory of the cells provided a field of choice, a variety of pathways along which the impulse might discharge itself as an appropriate or adequate reaction. But as we have pointed out, choice itself implies a loss in immediacy, a delayed reaction. Until the animal was provided with distant sense receptors it would have been fatal to it to have this power of delaying reaction. In an animal without a cortex action was dictated by the experience of all the animals of its species that came before it. To follow the wisdom or experience of the ages may insure safety but never progress. If the animal is to make any advances in behaviour it must use experimental procedure, and opportunity must be provided for preconsideration. This was the essential gift of the distant stimulus receptors.

Not only did the eye and the ear and the nose render delayed reaction safer, but they also gave richness and variety of experience to the animal. While for its experience of the world in which it lived it was dependent on the more primitive sensations and on a chemical food sense, it was decidedly limited in its opportunities for development. The distant stimulus receptors multiplied a thousand fold the stimuli crowding in upon the brain. But in estimating the rôle which the exteroceptive organs played in the building up of the cortex we must beware of over-estimating this richness of experience. We have referred many times to the relevant stimulus and have pointed out that though there is a multitude of things within the visual range of the goldfish in the bowl it is apparently blind to almost all of them. Why, we might ask, is this so? The answer is really simple—the goldfish *is* in a bowl. The stimulus remains irrelevant if the response is and must be inadequate. We may put this in another way by saying that we are insensitive to those things in our environment to which our response is irrelevant. The picture on the wall is part of my environment because I can include it in my behaviour patterns. I can put it up or take it down or break it to pieces. I can buy or sell it, imitate it or deface it, value or despise it. The picture has meaning for me because I can take some action regarding it. But to the goldfish it can have no such relation. The presence or absence or even the existence of the picture can make no possible difference to the fish and hence it is something which is never attended to by the animal. If the stars overhead never had any relation to our actions it is extremely probable that we should be blind to their presence. As it is we attend to them only because we have been told about their distance, magnitude or character, or because they are useful to us as weather signs, indicating a clear sky or otherwise, or to the mariner as guides to navigation. How much do you suppose the average man knows about their nightly appearance? He does not know how many there are or how they move, and with the exception of a striking constellation or two, knows absolutely nothing with regard to the pattern of their arrangement nor the names which other men give them. If all the stars were suddenly blotted out of existence, and nobody proclaimed the fact, it would take some people months and possibly years to discover it for themselves. The moon, being much more relevant to our actions, would probably be missed by most people in a couple of months, even though its appearance is not a constant phenomenon. But as regards the stars the average man is in about the same stage of observation as the very young child. Indeed, if these heavenly bodies had not been pointed out to some people when they were children one doubts if they ever would have noticed them at all. As a matter of fact, the stars play about the same part in the lives of most of us as the picture on the wall does in the life of the goldfish. Yet every man knows his dollars by their thousands while remaining entirely—and blissfully—ignorant of how many stars he, with the rest of mankind, numbers in his constant possession. We have used the term "blissfully ignorant" because after all there is no good reason why men should be set to count the stars. The reason why we know so little about the stars is because they can affect us so little and there is so little we can do about them. When people misguidedly believed that the stars in their courses had something to do in ruling men's destinies they probably knew very much more about them than the average man knows to-day. Yet the average man's knowledge of other things within his ken is immeasurably wider than such knowledge was at the time when astrology was believed to be a science.

This brings us back to our original conception that the distant stimulus receptors were not nearly of so much use to man as regards increasing the wealth of his experience as they were in making the world safe for cortical reactions. Many invertebrates such as the crab and the spider have wonderfully developed sense perceptors but have remained blind and deaf to thousands of things to which the higher animal attends. Variety of experiences, and hence greater exercise of the choice reactions, could only be provided if the power of movement, or going to and fro upon the earth kept pace with the development of better sense receptors. Some animals are almost as truly anchored in their environment as the fish is confined in the bowl, and environment has no relevancy to these creatures except in so far as they can act in regard to it. Though it may be a blow to our pride we must recognize that we ourselves are probably merely shadows to the goldfish and in time, since it cannot escape us or do anything about us, we may cease to be even that. Its very confinement or restriction of movement will tend to make the goldfish blind, nor would the case be so very different with us in like circumstances.

Just as the deaf, dumb and blind would be entirely dependent for survival on the distant stimulus receptors of other people, so also a man would be dependent for survival on the free mobility of other persons if he were permanently confined to one area by being fastened to a post with a chain. How much would he of his own initiative learn under these conditions? What need would he have of a cortex if his field of choice were so definitely narrowed? He too would develop the intelligence and learning habits of the goldfish. Obviously a vegetative organism must be entirely dependent upon the stimuli which come naturally and inevitably within its range. Telescopic vision, for example, would be of comparatively little use to a man unless he could ascend some eminence, however slight, from which to use it. It was a great advance when the animal by its own movements could seek its own stimuli. Fundamental, therefore, to the development of a higher functioning nervous system were better means of locomotion—legs, wings, fins and the like. Going to and fro upon the earth meant not only a greater geographical range and a better food supply but a greatly increased variety of experiences and range of discriminative sensitivity (to which distant stimulus perceptors contributed) and greatly increased mobility. In short, development consisted merely in an expansion of that original equipment of sensitivity and mobility which we found inherent in the amoeba. The result of development of this equipment was to add depth and width to the animal's experience—depth through the heightened sensitivity of the external nervous system and width by the enlargement of experience and choice which the power of rapid movement conferred. Even in our day and age it is noteworthy that man's progress is still along these lines. He has invented the telescope, the microscope, the telegraph, the telephone and the radio to add range and intensity to his vision and hearing, and the steam engine and the automobile and the aeroplane to increase his mobility.

But if increased sensitivity and wider movement were the essential advances leading up to the development of a cortex why was it that Nature had to await the evolution of the vertebrates, since many of the invertebrates possess these two capacities? The answer is that Nature's first and chief concern was the preservation of the individual and that this had to be provided for before the higher gift of the cortex could be bestowed. As far as bodily development is concerned the invertebrate was still in the plastic experimental stage. There were no limits to the number of legs or of eyes or ears as well as all sorts of special adaptive devices that these animal species could develop. The old moulds were easily broken and new ones as easily re-fashioned. But the greatest defect inherent in the invertebrates' structure was that they *were* invertebrate—they lacked the rigid internal framework upon which an adequately sized body could be built, or if, as in the case of the giant squids, they became of large size they could never become land-dwelling animals. If they remained soft bodied, then despite the development of special protective devices such as poison fangs or stings, they were comparatively defenceless. If on the other hand they became armoured they lost their sensitive outer surface and at the same time reduced their celerity and range of movement. Hence for their preservation they must rely on one of the most primitive methods —that of over-production. Considering the number of spiders that are hatched by one adult female does it not seem strange that we do not have a plague of spiders? The fact that they do not exist in overwhelming numbers is proof of their comparative defencelessness. So helpless are they that many of them are condemned to a life of nocturnal activity which ultimately is a hindrance to progress. For the invertebrates whose average life span is short and who owe their continued survival to multiplicity of numbers, the instinctive adaptations of behaviour are all sufficient. Why should such a wonderfully complex mechanism as a cortex be wasted on an animal whose chances for exercising choice will be so limited? It will not have either the time nor the opportunity to use the new powers that a cortex implies. Because of the inadequacy of provision for individual self protection and the limitations of size that an invertebrate body imposed, the making of the cortex had to await the development of a better body in which to function. A great stride forward in evolutionary progress was accomplished when Nature hit on the expedient of replacing the external armour by a bony skeleton within the body of the animal. Even when we come to the stage of development of the lower vertebrates we still find them too poorly endowed in other respects to deserve a cortex. With improved mobility came a wider geographical range for the individual, which was then subjected to rapidly changing conditions of climate and temperature. Again it may be well to emphasize the fact that the cortex was, par excellence, the organ which made individual adaptations possible and that it was therefore the environmental conditions which the individual had to face which were of so much importance. Apparently the individual animal organism can be adapted to the extremes of either heat or cold but sudden changes in temperature present a more serious problem in adjustment. The blood of the lower vertebrates, such as the fish and reptiles, varies with the temperature of their surroundings and by reason of this their range of movement is exceedingly restricted. The animal must live in the water where the range is not relatively great and where more even temperature conditions may be found by migrating a few feet to different depths. In any case the range at any season between surface and lower depths is rarely more than about 40 degrees.

In the case of a land animal such as a snake it must either be confined in its habitat to tropical forests where the temperature variations are slight, or it must find shelter when the seasonal or the diurnal temperature varies considerably. As in the case of the fishes the easiest migration is downwards rather than in a lateral direction. During winter then, or in the cold of night the animal must seek a suitable hole in the ground, and this when found is rarely deserted. A familiar background seems essential to the animal's well being. Just as we are ill at ease in strange surroundings so the animal is deeply disturbed by any unlooked for change in its usual habitat. The snake uses the same hole season after season while the seal will battle furiously for his particular place in the sun even though there may be thousands of other places just as sunny. Touching a bird's nest is often fatal to the young, as the parents will frequently desert them. The human taint has destroyed the familiar background and to the mother bird these are no longer her nestlings. In all probability this factor of familiarity of background is important as forming one basis for the young-protective habit and in part for the gregarious impulse. Patriotism, love of country and home, are of course entirely dependent on this factor of familiarity. Anyone who left home or country at a very early age cannot have any deep-seated love for them. Indeed the best corrective possible for a jingoistic imperialism is to live under another flag long enough to become thoroughly familiar with the new surroundings.

We have previously suggested that this desire for the familiar physical background is part of a general conditioning process. Just as the animal clings to the house or the den or the woods in which he has fed and has enjoyed the other satisfactions incidental to his existence, so the familiar physical background becomes a part of the general stimulus pattern of our behaviour, and if we are forced to change this background we are out of joint and ill at ease.

Because instinctive behaviour fills so much more of the animal's range of behaviour than it does of ours it is the more closely anchored to the one spot. So much of man's environment is internal—his memories, imagery, etc., which he can transport with him wherever he goes—that to some individuals any place is home; but that is not true of the animal. To the free-ranging, warm-blooded animals this matter of anchorage in the one spot is considerably less of a factor than it is to the so-called cold-blooded reptiles. For the former it is only during the mating and reproductive season that all their activities radiate from one geographical centre but for the latter this is the case all the year round. Birds and mammals are limited as regards their habitat only by their hunting and feeding range, but the reptiles' wanderings must have as their constant centre their own familiar shelter or home. The effect of cold on these animals is to retard all of their vital processes so that they become torpid and inactive. During winter they must hibernate, and both seasonally and diurnally the necessity of finding a shelter anchors the reptiles very definitely to one locality. As regard man the same consideration was undoubtedly one serious factor in his lack of progress during the long period before his invention of clothes and fire-making made him independent of the caves and rock shelters, the possession of which he disputed with the cave bear and the hyaena.

The term for animals whose temperature varies with the surrounding medium is "poikilothermic" and for those whose temperature remains constant the name "homoiothermic" has been employed. As substitutions for these unwieldy terms we would suggest "thermovariant" and "thermostatic." Birds and all mammals belong to the warm-blooded or thermostatic group while the reptiles and fishes make up the thermovariants. Among the first group man has a blood temperature of about 37 degrees Centigrade, while in the wolf it ranges as low as 35·25 degrees. In birds the temperature is as high as 44 degrees Centigrade, while in the monotremes which include the echidna and the duck-billed platypus the blood temperature is thermostatic only between 20 and 35 degrees.

Now it is obvious that as regards range of adaptability the thermostatic animals have decided advantages. A high blood temperature means a more rapid circulation and more effective heat regulation. The effect of cold on the thermovariant animal is to make it sluggish and inactive, while the thermostatic animal is stimulated to exercise and movement.

The thermovariant animals being anchored to their environment remain slow-moving, belly-crawling creatures, especially if exposed to the diurnal and seasonal variations of climate as in the temperate zones. They are heat loving because high temperatures are optimal for their activity. In response to the mating impulse they may wander far afield, but in all probability the range of journeyings of a snake or lizard in a whole year does not equal that of some of the carnivorous animals in a single night.

But to a rapidly moving animal a swiftly coursing blood stream is necessary not only as a heat regulator but as a carrier of oxygen to the muscles. The cold-blooded animal is not therefore adapted to prolonged celerity of movement. In lizards and snakes the foraging for food is mainly a slow-moving, waiting-in-ambush affair in which capacity for long periods of immobility is as much a factor in success as rapidity of movement. The birds on the other hand exhibit extreme celerity of movement and hence have the warmest blood stream.

How great a threat to life swift changes in temperature constitute will be realized when we consider the very special devices with which even animals in tropical regions are provided. Some of the carnivora and many of the tree-living animals possess thick fur. In order to carry this increased insurance against cold they are forced to become nocturnal in their habits and to spend the hours of sunlight in deep shade. The mammals which live in high latitudes must either have very thick fur or enormous stores of blubber which make them slow and unwieldy on land. Even so some of these must imitate the reptile and hibernate during the winter.

Of what use then would a highly developed cortex have been to a cold-blooded or thermovariant animal, restricted to life in tropical forests or to nocturnal habits, or else, if living in temperate zones, forced to hibernate for months? Man with his naked, furless body and his comparatively slender bulk would have been under such circumstances wholly at the mercy of his environment. The whole of the temperate zone would have been closed to him and he would have been condemned to life in the tropics, where most of the day would have been spent in the depths of shady forests and the rest of his time seeking shelter from the dampness of tropical nights.

We little realize how favourable to the functioning of a highly developed cortex the temperate zone really is. It alone provides the conditions which act as an incentive towards forethought and planfulness. There season follows season in due order so that there is the time for ploughing and sowing and later on for ripening and harvest. This seasonal variation enforces on man a degree of forethought in the adaptation of means to an end. It is the very uncertainty of conditions which makes variability in the animal's response advisable. In the tropics, on the other hand, there is no marked seasonal variation; seed time and fruiting overlap, food is always plentiful and there is no need for forward-looking, anticipatory reactions.

Lest we seem to be paying undue attention to the influence of environmental or climatic conditions it might be well to glance at the character of races inhabiting widely different climes. The race which has been cradled in the tropics or sub-tropics where sustenance is easy, through the profusion of plant and animal life, has but little need to develop prudence and forethought. Life is so easy going that the new situations which must be met and grappled with are comparatively few. The attitude or temperament which is developed under such conditions is pliable, happy-go-lucky, improvident and retrovert. The easy-going suggestible nature of many sub-tropical races is well known, especially where there has not been the spur of over-population. On the other hand what a marked contrast in character we find exemplified in the Scotch on whom the hard rigorous climate and soil conditions of their country have imposed a caution and farsightedness that have become deeply ingrained in their national temperament.

The Esquimaux who must cope with the severe and long-continued winter of their high latitudes are even more handicapped as regards variety of experience. Their temperament must be that of the unenterprising, stolid, apathetic type with infinite capacity for patient endurance. For them the already tried and proven expedients of their race are the only safe models of conduct, and the man who steps outside the bounds of that racial experience may pay for the experiment with his life. A poorly developed cortex may be sufficient to enable a man barely to maintain existence in high latitudes but the distinctively human cortex assuredly did not develop under those conditions. The man in the tropics has little need to experiment, to make choice of alternatives, to use preconsideration and forethought while the man of the snows finds life so restricted that it is not safe for him to experiment. The temperate zone provides multiplicity of experiences and the time and opportunity for experimental procedure. It was the zone in which the human cortex found a suitable field for its most typical form of functioning.

A thermostatic blood temperature is, as we have seen, one of the bodily adaptations favourable to a free and unrestricted life in this zone. Through the inventions of fire and clothing man made himself still more independent of climate and was able to extend his range north and south over wide areas. Incidentally, too, he was able to increase the period of his diurnal activities. It is to a day-ranging animal living in the temperate zone that a cortex organized for response to a multitudinous variety of experiences is most useful.

It is perhaps noteworthy that downward changes in temperature seem to constitute the greatest threat to life. Animals may have sweat glands, and other devices such as the exposure of mucous membranes to the air in order to diminish body heat, and among natural heat regulators shade and water may be constantly used to modify high temperatures. But of natural means of protection against cold man has singularly few. The only way in which we can become warm is by exercise, but this is only a temporary expedient since exercise finally induces fatigue so that exercise must be followed by a rest period. But where Nature cannot protect she can at least warn. Hence we find our body surface not only sensitive to cold but what is more important, we have a most retentive memory for cold. Long after the stimulus has been removed we retain the characteristic sensations. This is evidently Nature's way of impressing the experience on us and is the means she employs to warn us that an external condition exists which is inimical to our survival.

CHAPTER LI

NEURAL CROSS-ROADS

Any change in the external environment which adds a new element of complexity to animal behaviour may be considered a step towards the ultimate building up and functioning of the cortex. It was a great advance when sensory placodes were developed, since these served as guides to movement and added the first element of choice of direction to the hitherto blundering and haphazard journeyings of the animal. It was also a decided gain when sex was added as another drive to action for in the wake of sex came all kinds of structural and behaviouristic changes that have their place in our make-up and conduct to-day. Though sex is by no means the whole of life, nor indeed more than a fraction of the psycho-analytical faddist's idea of it, it is nevertheless an extremely important factor in our development.

It was a further gain when sensory placodes developed into distant stimulus receptors and when the animal became possessed of an internal bony framework instead of an external skeleton. Another long stride forward was accomplished when animals became land dwelling and thus came in contact with an immensely wider range of potential stimuli. The story of development was already half told when the animal was able to lift its belly from the ground and coincidentally with a greatly increased mobility became also warm-blooded or thermostatic and thus adapted to a wider climatic range. We have seen also how much it profited the animal when the fore-limbs were released from the business of locomotion and became the chief handmaidens of learning, the examining, holding, tool-using organs. This development of the hand gave an entirely new importance to the sense of touch, part of our original equipment which had become rather dwarfed in significance owing to the importance of the more newly added distant stimulus receptors, the eye and the ear.

But the increased capacity for movements both skilled and unskilled, necessitated a much more complicated neural communicating system. Hitherto we have been considering the effect of various bodily adaptations outside the central nervous system. We must now take stock of the changes which occurred to keep pace with the complexity of bodily movement.

We have seen in Chapter XXXV that there is a variety of combinations of movements that the four-limbed animal carries out. All of the limbs may act together or the front and hind limbs alternately in pairs, or the front and hind limbs on opposite sides may synchronize in movement—all of this according to the kind of animal and the gait it happens to employ. Now it is evident that once the animal has assumed this bilateral and contralateral movement, the one side of the body must be constantly informed of what the other side is doing. The scriptural injunction about not letting your right hand know what your left hand is doing is without force in neurology since anatomically speaking that is quite impossible. The right hand must know of the position and movements of the left hand or manual co-operation would be impossible.

From the earlier chapters of this book we have learned how tremendously complicated muscular movement really is and how, in order to co-ordinate these movements, there must be a constant stream of informative impulses flowing along the proprioceptive pathways to those portions of the brain which initiate the movements of locomotion. Whether the two limbs are to move in unison or whether they are to be moved alternately, the position in space of each must be ceaselessly telegraphed, so to speak, to the motor initiatory centres. If this were not so movement in either limb would be unequal. One of the kangaroo's hind legs might receive an impulse for a long hop and the other for a short one, or the quadruped in walking or running might take steps of unequal length. The result would be that the animal would move in a circle or have an altogether stumbling gait. Before the motor initiatory centres can command a movement they must therefore have exact information as to what the other side of the body is doing.

This necessity for proprioceptive information can be quite simply illustrated if we suppose that a person is blindfolded and required to carry out movements of the left hand corresponding to those made by the right hand, which is moved by the experimenter. The latter, in thus moving the passive right hand, is taking the place of the motor initiating centre for the right hand which is in the left side of the brain. Supposing the experimenter flexes the subject's right hand or carries the arm six inches to the left. What must happen before the blindfolded person can initiate these movements with his free hand? Obviously informative impulses must go from the right hand up the arm to the portion of the brain which controls the movement of the left arm and hand. As this is on the right side of the brain the informative impulses must go to the same side, i.e. from the right hand to the right hemisphere.

Now the value of these proprioceptive pathways, which serve to inform the animal of the position of its limbs in space and the flexion or otherwise of its joints, is patent—it sets the eyes free from the business of reporting the position of the limbs, and so, when the animal is moving, allows them to act in the way they were intended—as distant receptors, a function of great value to the animal in guiding its course and a rôle which we have seen is essential to the proper functioning of the cortex. But the establishment of these proprioceptive pathways necessitated a remarkable development in the ground plan of the neural system so that a dual communicating system could be in use, one the motor pathway crossing over from one side and initiating movements of the other side of the body, and the other an informative pathway running directly to the same side of the brain. The crossing over of the motor nerves takes place as we have seen at the decussation of the pyramids in the medulla and at different levels in the spinal cord.

In considering the reasons for this neural adaptation, its advantages may be realized if we consider what must have happened if the left side of the brain had controlled or initiated movement on the same side of the body. Such a condition can be illustrated diagrammatically in Figure 78. In this, RMI stands for the right initiating motor centre, and LMI for the left motor initiating centre, while LA represents the left arm or leg and RA the right arm or leg, the arrows indicating the direction of the nerve impulses. Now under these conditions of homolateral control and initiation, as soon as the right hand was flexed the informatory message would need to be sent up to the brain of the same side, thence through the commissural fibres to the other side of the brain before the left hand could carry out the corresponding movement of flexion. Obviously action would be somewhat delayed because of this circuitous route that the nerve impulses would need to traverse, to say nothing of the increase of complexity of the transmitting pathways in the brain itself. Mobility as dependent on quickness of co-ordinated action might under such an anatomical arrangement be very seriously retarded or impeded. Is there any way by which

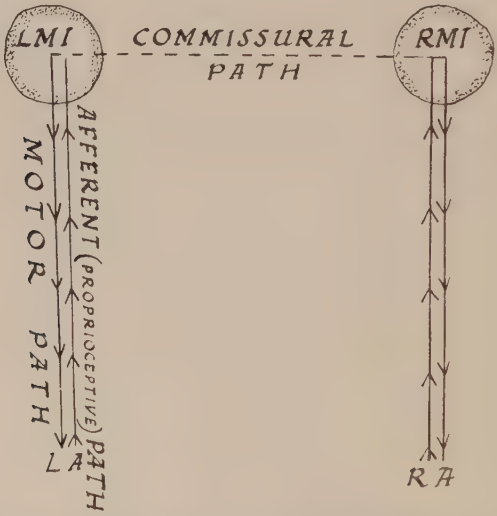


Figure 78.—Showing how, under conditions of homolateral neural control, proprioceptive impulses would require to pass through both hemispheres of the brain in order to bring about contralateral movements.

this proprioceptive or informatory pathway could be shortened and at the same time pursue its way without adding to the complexity of transmission or communicating network within the brain itself?

As a matter of simple mechanics, there is one solution of the problem possible—by allowing the motor pathways to cross over or decussate outside the brain itself in such a way that the right side of the brain could control the left side of the body and vice versa. Then by keeping the course of the proprioceptive pathways direct as before, that is to say, the informatory impulses from the right side of the body going to the right side of the brain, then the mechanism necessary for contralateral co-ordination of movements would be neurobiotaxically grouped in the central nervous system. The neural pathways would now be as pictured in Figure 79.

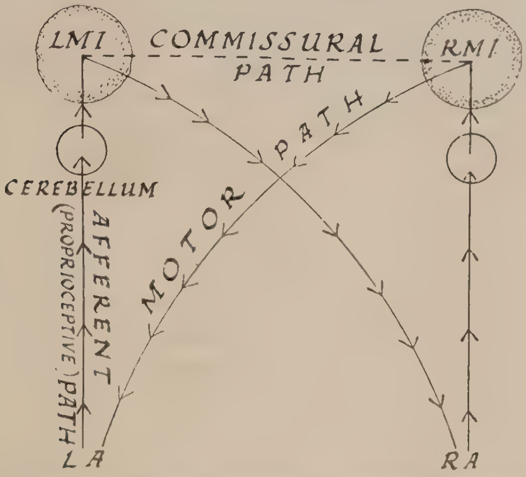


Figure 79.—Illustrating the neural pathways for contralateral movement of limbs. The hemisphere which receives the proprioceptive information from one side initiates movements of the opposite side by means of the decussating motor pathways.

Now when the right hand is flexed by the experimenter the proprioceptive impulses go to the motor initiating centre of the same side and it can at once initiate the corresponding movement of the left hand. But these proprioceptive impulses require a centre where they may be co-ordinated, a switchboard, mechanical it is true, but still a switchboard where by neurobiotaxically grouped pathways the impulse can be relayed to the proper portion of the motor initiatory cortex. Turning back to Chapter XXXII we find that an anatomical co-ordinating centre is provided in the cerebellum to which run what have been called the silent afferent fibres which do not follow the usual afferent course through the fillet and thalamus. Poise and balance and muscular co-ordination generally thus become the function of the cerebellum and may be effected without cortical intervention. By freeing the cortex and the eyes from co-ordinating locomotion, and thus allowing the contralateral control of limbs to be carried on through cerebellar pathways, the animal's attention may be directed towards other objects. It would be rather unwise to expect a captain to do his own steering.

But while the crossing over of the motor tracts outside of the brain insures that in contralateral movements the proprioceptive and the motor centres of opposite sides of the body should be neurobiotaxically grouped in the brain, what is the situation when one-sided movements only are in question? Supposing I wish to flex the fingers of the right hand, then I must know of their position. Since the movement is to be initiated from the left side of the brain the proprioceptive information should go direct to that side. This pathway is provided through a decussation which takes place in the brain stem. Hence we have two decussations, one proprioceptive, and the other motor in order to ensure the directness of motor control. In every movement of the limb then there are two sets of proprioceptive impulses streaming to the brain, the one going direct to the brain of the same side so as to correlate movements of the limbs of opposite sides, and the other a decussating pathway so as to bring about co-ordinated movements of the limbs of the same sides. Both of these sets of impulses probably pass through the cerebellum. The crossing of the wires, both proprioceptive and motor, confers an undoubted advantage both as regards celerity and accuracy of movement. In this way both sides of the brain can be informed simultaneously of any movement or change in position of any part of the body, and by the crossing of the wires at lower levels the central switchboard is kept from being needlessly complicated. The final situation may be illustrated as in Figure 80. This shows the direction of the two proprioceptive pathways and also the decussating motor pathway. This decussation of the motor pathways may be regarded as one of the fundamental requirements of four-limbed locomotion, and taken in conjunction with the functioning of the cerebellum as the co-ordinating centre in the whole neural arrangement, must be regarded as a long step forward in the way of preparation for a more highly functioning cortex.

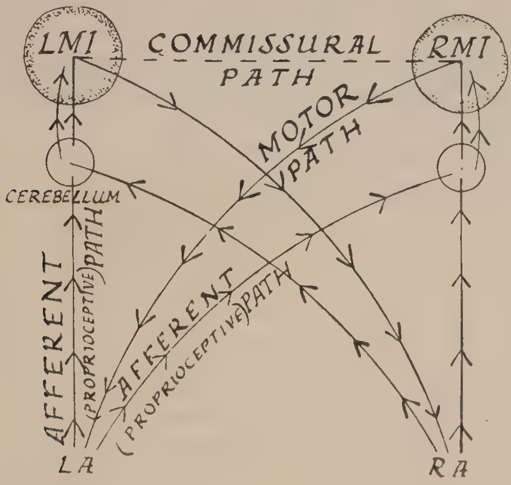

LMI
COMMISSURAL PATH
RMI
MOTOR PATH
CEREBELLUM
AFFERENT (PROPRIOCEPTIVE) PATH
AFFERENT (PROPRIOCEPTIVE) PATH
LA
RA

FIGURE 80.—Illustrating the neural pathways for contralateral and homolateral movements. Both hemispheres of the brain can be simultaneously supplied with proprioceptive information. The commissural path is kept free for other co-ordinating impulses.

The decussation of the sensory pathways also brings about a neurobiotactic grouping of the motor and sensory centres and thus ensures a ready and appropriate response to any stimulus affecting one side. Supposing a pin prick is applied to the skin of the right hand. The appropriate response is of course a withdrawal of the right hand. This must be effected by the motor centre of the left side of the brain. Hence in order to ensure this ready linking up of sensory and motor impulses the sensory path must also cross over to the left side of the brain.

CHAPTER LII

MONOTONY AND INTEREST

In considering the effect that an unusual occurrence has on animal behaviour we are at once struck with certain apparent contradictions. In very many of the invertebrates and lower vertebrates the unusual phenomenon brings forth no response from the animal. Other animals of similar evolutionary status, however, may respond immediately to an unusual appearance. All sorts of strange sights may surround the blind-worm to which it pays no attention whatever, yet we have noted the immediacy of its response to the relevant stimulus, the sound of rain-drops on the hard earth. The fiddler crab's reaction to the unusual is on the other hand quite different. Walk slowly across an area of mud and sand inhabited by these invertebrates and you are surrounded by an area of vacancy which moves with you and is caused by the popping down of crabs in front of you as you advance and the popping up again of the crabs behind you. Very many other invertebrates display an equal mental alertness when an unusual stimulus presents itself.

In the higher animals the excitement that the unusual stimulus occasions is very marked. According to Kohler chimpanzees may be thrown into paroxysms of terror by the appearance of some strange-looking animal such as a donkey or a camel. We are all familiar with the fright that the young child exhibits when someone familiar to him approaches wearing a mask. These are, however, cortical or discriminating fears. Yet the goldfish and the blind-worm show neither interest nor alarm at very many appearances which must have been entirely outside the range of their experience. In the somewhat lowly invertebrate, such as the slug, no interest in unusual phenomena, no matter how relevant, is betrayed. It is doubtful if a snail ever hurried its pace to avoid being trodden on.

In a previous chapter we have referred to one fact with regard to this matter and that is that the animal does not attend to the stimulus with regard to which it lacks all possible means of response. The fiddler crab or the spider responds to the unusual because he has developed means of locomotion that give him celerity of movement and distant stimulus receptors which give him warning. The blind-worm or the goldfish may have these receptors, but lacking a ready means of escape, cannot make an adequate response. In a sense the adequacy of the response to the unusual is thus the measure of the development of the animal whether racial or individual. In the chapter on facilitation we have attempted to explain how it is that the unusual or unexpected stimulus gains its prepotency so that it is able to capture our attention and to call forth a widely diffused response. In such cases, as we say, we are held spell-bound, the whole body being involved in the attentive attitude. But we have not yet considered the process whereby the constantly recurring or monotonous stimulus, though at first attended to, soon loses the power to call forth any response.

Instances of this process of habituation are common enough. When we enter a strange room we may at first be conscious of the clock's ticking, but after a little time we cease to attend to it, so that the stimulus, though recurring, calls forth no further response than that involved in the first recognition of its occurrence. If the clock stops, however, we may become aware of the fact. Some would explain this obliviousness as due to fatigue or failure of the sensory mechanism, but this is unlikely. Another explanation sometimes put forward for this phenomenon is that we really hear the clock's ticking all the time with our unconscious mind which informs our conscious mind of the cessation of the noise. This explanation, though glib enough, is ridiculous. Hearing presupposes listening, and that would mean that in order for us to listen unconsciously but not consciously, we should require a separate set of cerebral mechanisms through which our unconscious minds could function. But this is not the case. There are, however, degrees of attention and we may be at times so dimly aware of some sensation that it is difficult to say when we have actually ceased to attend to it. In this sense the sensation may be called subconscious. That activities once learned can be carried on through some "lower brain level" is an assumption without any basis of fact. Once a nerve path becomes facilitated it tends to remain so, and to suppose that the impulse could be relegated to some lower level pathway would mean a new set of neurological hypotheses to account for psychological phenomena. The goldfish also attends to certain recurring stimuli at first, but gradually becomes insensitive to them. It may, for example, respond by swimming away if you approach the bowl, but eventually it apparently ceases to see you. This lack of response does not mean of course that it sees you subconsciously or unconsciously, nor can it be attributed to any process of reasoning on its part. The explanation of this habituation to the recurring or usual appearance must be sought on other grounds.

The stimulus to which we can become habituated may have qualities of greater intensity than the ticking of a clock, provided, of course, that it is monotonous or rhythmical or constantly recurring. Workmen in factories where there is a great deal of noise will sometimes complain that visitors, especially women, yell at them in conversation, instead of employing an ordinary tone. They are so habituated to the roar of machinery that they really do not hear it. If for any reason the rhythm changes or if they listen for the sound they are at once sensitive to it.

When we wake up in the morning we may respond to the presence of daylight with the thought either vocalized or sub-vocalized, that it is light, but once the day's activities are begun we make no further response to this particular stimulus even though it is constantly present.

Obviously it would be decidedly disadvantageous to us if there were not some way to side-track or otherwise neutralize these recurrent stimuli. If we listened to the clock all day we should not have time to do anything else. If the roar of machinery continued to have its initial effect on the worker he would soon be a nervous wreck. Country people would never sleep in the town nor would travellers on trains get any rest if it were not for this process of habituation.

What, then, is this process? How do we come to attend less and less to the stimulus which because of its regular recurrence has become irrelevant? Is it a cortical, peripeheral, or conducting condition? Apparently we are on safe ground in assuming that it is cortical. It certainly is not dependent upon any condition such as fatigue of the sense receptors, since immediately the clock's ticking is brought to our attention in some way we have no difficulty in hearing it. If, for example, it suddenly occurred to us that the ticking did not come from a clock but some explosive mechanism, then we should hear it most acutely. That the conducting mechanism, the sensory nerve fibres, should vary in their efficiency is also extremely unlikely. It is no part of the work of the conducting fibres to discriminate between stimuli. There are in fact a great many recurring stimuli which are so relevant that they must be attended to. The pit-a-pat of raindrops is monotonous enough, but the blind-worm must immediately respond to it. It is neither familiarity nor recurrence which is the measure of relevancy. Because the bell summons us to meals or lectures with monotonous recurrence is no reason why we should attend less and less to its call.

If the process of habituation is cortical then in all probability we must look for its explanation in some change in *relative* synaptic resistance. We have seen in a previous chapter that the passage of an impulse along a nerve path lowers synaptic resistance so that the next impulse of the same kind finds a facilitated path of discharge and hence the response to the second stimulus is so much the readier. Evidently if we depend entirely upon a theory of synaptic resistance automatically lowered by repetition, we should expect a continued response to the recurrent stimulus and in fact one that becomes progressively easier. But as we have seen, a recurrent stimulus may be reacted to once or twice and thereafter have no power to evoke any response at all. We require an explanation which assumes that synaptic resistance is gradually built up, either absolutely, or in relation to the synaptic resistance of pathways leading to other forms of motor activity and discharge.

But ordinarily speaking, absolutely heightened synaptic resistance means a greater degree of accompanying consciousness, a damming back of neural energy and a diffused response, as for example, if some new element is introduced into a familiar motor activity, we must give it our attention until we learn the process. But since attention diminishes with habituation we cannot assume that synaptic resistance is the cause of the blocked or side-tracked response. We are then left with the idea that the resistance is only relatively higher, that the potency or relevancy of the recurring stimulus is less than that of others coming in at the same time, and which, in a manner of speaking, drain off the neural excitation. From one point of view we all have single-track minds in the sense that we have a great difficulty in attending to two things at the same time. We may of course knit or walk or play the piano and attend to other matters simultaneously, but that is only when knitting or walking or playing the piano have become so facilitated that we do them automatically, leaving us free to attend to other things. We have known or heard of people who could do two things, such as adding two columns of figures at the same time, but there is some reason to doubt that the attention is really divided. The probable explanation is that in such operations we alternate our attention very rapidly between the two activities. Generally speaking we may say that impulses seem to have their right of way singly over the nervous system so that we attend to one thing at a time.

We have also seen in our reference to the conditioned response that if an indifferent stimulus occurs simultaneously with some very relevant motor reaction with which it is not causally related, it may come to serve as the cue which calls forth the reaction; as for example, the sounding of the dinner bell synchronizing with the presentation of food, will, after a time, be sufficient to call forth the response of a flow of saliva in the dog's mouth. This does not mean that the conditioned stimulus, the bell, takes the place of the relevant stimulus because of course the sight of the meat without the bell will call forth the appropriate reaction. What happens is that the bell sound, having no appropriate response of its own, by constant association enters into the more relevant behaviour pattern as part of the stimulus and as soon as it is presented to the dog's consciousness the saliva begins to flow. But if the bell is sounded often enough without the appearance of the meat there is a deconditioning process so that eventually no response will be evoked.

In the process of habituation something similar occurs. We have a stimulus which, because of its monotonous regularity, needs only be reacted to once and thereafter not at all. The sound of the bell does not of itself fit into any behaviour pattern. There is nothing the dog needs to do or can do about it; there is no adequate response. The stimulus is therefore irrelevant or of only minor relevancy. The ticking of the clock is in the same case—it is of very minor relevancy so that there is nothing that we need do with regard to it. Consequently when simultaneously another stimulus is presented which has more relevancy, which calls for more adequate response, or which fits into a behaviour pattern in which each reaction serves as a stimulus for the next, thus forming part of the activity stream, then the stimulus of minor relevancy is side-tracked and isolated out of that stream so that it no longer has power to call forth a response. The synaptic resistance has not been absolutely but only relatively increased in relation to the path of discharge of the more relevant stimulus. In mechanical terms we may say that the neural energy will not continue to flow along these synaptic paths because new incoming stimuli find a more open, or to use an analogy from irrigation, a lower-level channel of discharge. We no longer hear the clock tick, not because it has lost absolute potency but because it has been crowded off the stage of attention by the more relevant or prepotent stimulus. If the ticking of the clock were the only stimulus present we would undoubtedly attend to it considerably more. To a man confined in a solitary cell a clock would seem a noisy piece of mechanism.

In ordinary circumstances the sound may be a stimulus powerful enough to evoke a response either vocalized or sub-vocalized, but having made this response we have no need to pay further attention to the fact unless of course something happens which sweeps the isolated occurrence into the activity stream as part of a wider or more relevant behaviour pattern. In the hall near the room where I work all day, there is a gong which sounds every hour to mark the lecture periods. I doubt if I hear that gong more than once a week or possibly once a month. I do not go to lectures so it is not part of my activity stream. To me it is not a signal for anything and consequently I am insensitive, or as we might say, absent-minded towards it. Probably I only hear it when it sounds at a time when my attention is for the while not engaged with other matters. The only time at which I hear the gong regularly is when I am working on a holiday. Then I hear it because it sounds so much louder against the unusual stillness. The intensity of the stimulus is changed, involving a larger area of cortical excitation, and thus it compels attention. The gong, however, does definitely enter into the student's activity stream and he cannot afford to be absent-minded with regard to it. Absent-mindedness is a process of over-inhibition. Attention is so occupied with responses to one set of stimuli that other stimuli of equal relevancy cannot force themselves, as they should, into the activity stream.

In some cases the recurrent stimulus, if important enough, may become by a process of conditioning part of another stimulus-behaviour pattern. The workman who is habituated to the noise may work better if the machinery is going, the city dweller may find the country too quiet for rest, or the stopping of the train on the transcontinental journey may wake the traveller up. Even the ticking of the clock may enter into the background of our actions so that we are aware of the fact when it stops. Some such conditioning process by which the stimulus becomes part of a more relevant behaviour pattern is necessary to account for such a fact—otherwise how could the cessation of a stimulus to which we are already deaf have power to force its way into consciousness?

Perhaps it would be better to say that such a stimulus is only very weakly or partially conditioned. There is no such marked conditioning as in our example of the sound of the bell serving to bring about a flow of saliva in the dog's mouth. The ticking of the clock by itself does not serve as a cue for anything else to occur. Possibly the presence of daylight is a stimulus to us to continue to work ere the night cometh, and as such enters into our behaviour patterns. But quite evidently the process of conditioning is only marked when there is a great difference in relevancy between the indifferent stimulus and the rapidly following unconditioned stimulus with which it is constantly associated, as for example, between the sound of the bell which means little or nothing to the dog and the presentation of food, which means a great deal. We have also seen this exemplified in racially conditioned responses where one reaction is captured or incorporated into the more relevant sequence; as, for example, nest building has been cut off from its original stimulus because it was of far more importance in the reproductive sequence than it was as a concealment device. But if two stimuli are of equal relevancy one is hardly likely to be incorporated into the other's behaviour pattern. Similarly with the raindrops' pit-a-pat which is a racially conditioned reflex in the blind-worm. If for any reason the sound of the rain was to any degree a call to the blind-worm to seek shelter it would never serve as a dinner bell to wake it up to go and look abroad for slugs. It was only because the raindrops of themselves meant so little to *Anguis fragilis* that they became by conditioning part of its stimulus-behaviour pattern. In the same way the workman ceases to attend to the noise of the machinery because there is absolutely nothing he can do about it, whereas if he could control the sound he would continue to hear it. We become domestically deaf because we can or think we can, afford to be so. The wife's remarks appear to call for no response and so she does not get any. If too, we were responsible in some way for regulating the amount of daylight received, we should always be actively conscious of it, for it would then enter into our activity stream.

The process by which we acquire new motor skills is different from the process of habituation. In the former we have a continuous or recurring stimulus but the response does not end with itself, it is not isolated but enters closely into the activity stream; the skill when acquired has value or relevancy to us and hence the response is continued. The stimulus is in this case the wish to learn. In the acquiring of a new motor activity there is a progression in response from the unusual to the usual. Our first response in a new complex motor activity is not an adequate one and consequently the neural energy is not wholly discharged. According to the theory advanced in Chapter XLVIII the unexpended neural energy is returned by a counter current reinforcing the excitation of the already sensitized cells. This excitation spreads over new areas involving other motor responses until the appropriate path of response is found. The diffused excitement is accompanied by a heightened degree of consciousness and an involvement of the senses in the bringing about of the correct response. When the most appropriate response is found, this becomes the facilitated pathway, the area of diffused excitation is reduced, the senses are set free from the business of guidance and direction, attention is thereby relaxed and consciousness, except in a much-diminished degree, no longer accompanies the reaction, so that it becomes, as we say, automatic. This does not mean at all that because consciousness does not accompany the act that its control is thereby relegated to a lower neural level. All that is meant is that the path of response has become so facilitated that synaptic resistance tends to disappear and with it the conscious direction of the activity, leaving us free to attend to some other activity. We can do several things at once but can only attend to one thing at a time. The animal's response to an unusual but relevant situation has some points of similarity. Whether it be the prick of a pin or some sudden unexpected appearance or intense sound, the stimulus finds a prefacilitated path. The impulse reaches the motor nerve endings with undiminished energy calling forth a very widely diffused motor response. Even the most violent but momentary reaction is insufficient to discharge the neural energy adequately and there is an immediate counter-current returning to and augmenting the sensitivity of the already excited nerve cells. There is a diffusion of excitation to wider areas involving the cortex which now initiates action, so that we pass from the subcortical start of fear to the cortically controlled flight, defence, or attack. It may be, however, that the cortex through memory recognizes the startling situation as being really irrelevant and modifies the response accordingly. This modified response may take the form of a vocalized or sub-vocalized comment on the situation. When we realize that it was the cat and not a burglar which made the noise in the hall our alarm quickly subsides. Even this may, however, prove an inadequate discharge, as we may continue the trembling and other physical accompaniments of excitement long after the situation has been reacted to and has passed. These motor manifestations evidently represent an overflow of undischarged neural excitation. If nerve impulses are undischarged in motor responses what becomes of the excess energy unless it is returned to the cortical centres?

Some such theory as that of neural counter-currents is useful as a working hypothesis to explain how reactions come in series, one apparently serving as the stimulus for the next. If the stimulus were to discharge itself all at once by one limited path of response we could have no sequential or co-ordinated movements such as in muscular movements, but merely a confused and undirected activity. According to our theory the impulse pursues the most facilitated path to the first muscles or set of muscles involved but is only partially able to discharge its neural energy. There is at once a counter-current set up and since by reason of their refractory phase the same muscles are incapable of reacting again immediately, the impulse discharges itself along the next most facilitated pathway to other muscles until the whole sequence having been worked through and the movement completed the neural energy is spent. In order to illustrate this process we may liken the muscles to the keys of a keyboard, which tend to remain down for a certain period of time when struck. The neural energy cannot thus be expended in repeated movements of the one key, but must proceed to the next key, which in turn has its refractory period, necessitating the passing over of the stimulus to the next key till the movement is complete. It is the direction of the diffusion of excitation which determines the order in which muscular contractions shall take place and this may explain why the site or localization of the previous stimulation has influence in determining what muscles shall be activated next. Whichever muscle or set of muscles receives the stimulus first will naturally react most strongly to the neural impulse so that the rôle played by the particular muscle will depend very largely on its place in the series and the point, anatomically, from which the neural energy begins to be diffused.

Hence one muscle may be involved in several movements acting to a different degree or in a different capacity in each. This is of course advanced merely as a tentative theory since we have no actual proof that such neural counter-currents really exist, so that like the theory of synaptic resistance it must be used merely as a working hypothesis, but one that seems to fit the facts. Anatomically there is nothing against the theory. We have seen in an earlier chapter that the motor nerve is not purely motor but that one-third of its bulk may be made up of afferent fibres representing a neurobiotaxical grouping of neuraxons. Hence there is provided the necessary mechanism for an overflow or counter-current of unexpended neural energy from the muscle back to the area initiating the movement. Accepting the theory would mean that a new factor could be brought in to help to explain how stimuli are apparently differentiated and how the adequacy of the response determines the potency or relevancy of the stimulus. The situation, which can be disposed of adequately by some limited or specific path of response, will result in the total expenditure of the neural energy called forth by the stimulus. There will then be no overflow, or neural counter-current, and no diffused excitation. Consciousness will therefore not be associated with the reaction and it will cease to be attended to.

Coming back to the animal's response to the unusual we may still need to account for the lack of response in some of the lower vertebrates even though the stimulus may have relevancy. The explanation is that some animals do not have cortex enough to attend to the new and unusual. What motor cortex such animals possess is probably taken up with the already facilitated paths of motor response. When the new stimulus presents itself there are neither prefacilitated paths nor other levels of neural structure to which the energy can be diffused. It is only in the animal with the more complex cortex that any choice of reactions is possible. The provision of the cortex thus will enable the animal to increase the range of stimuli to which it can attend. The animal of simpler neural structure proceeds along the well-worn paths of ancestral response and all the phenomena for which there are no ready-made reactions are simply disregarded. The cortex, then, has given man more things to fear but it has also provided him, through its action, with more ways of escape. It has multiplied the number of adequate reactions and at the same time has increased the range and number of effective stimuli. We must remember, however, that it is the adequacy and value of the response that determines the efficiency of the stimulus. The recurring irrelevant stimulus is either side-tracked or conditioned. The animal of simple neural structure will only attend to the stimuli to which it has the means of response.

CHAPTER LIII

SENSE OF ALIVENESS

The development of the cells of the cortex with their specialized ability to retain more or less permanently the effect of impressions was responsible for a great advance in animal behaviour. New complexities of structure resulted in new adaptations, new complexities in behaviour. The power of choice was very greatly extended. Action was no longer dictated wholly by the past experience of the race but choice was largely influenced by the individual experience, for individual experience was now recorded in the central nervous system in the form of newly facilitated nerve pathways. The built-in habits of the race became of less significance than the built-up habits of the individual, though the whole of mental activity rests on a mnemonic basis.

It is cortical memory which gives to consciousness its peculiarly human value. Up to this time we have said very little of consciousness. The term itself is commonly used rather vaguely, many people saying that they are conscious of something when they really mean that they attend to it. Consciousness and attention are such closely related aspects of human behaviour that to some it appears as if they were synonymous. The question which naturally arises is whether we can be conscious without attending in some degree to something. Without attempting at present to settle the question as to whether consciousness and attention are the same thing, we shall continue to use both terms. Some psychologists are advocating dropping the former altogether.

Even the lowliest animal with the simplest kind of structure must have at least some germ of consciousness but this is almost certain to be no more than a sense of aliveness, or flashes of what we may call awareness. But without a cortex and cortical memory there could hardly be any continuity or connection between these flashes, no stream of activity or flow of consciousness. We have seen that as regards the cells of the external nervous system, a capacity for prolonged retention of the effects of stimuli might be of positive disadvantage, but with the building up of a cortex we have memory added to awareness, the forging of the links between experiences so that the individual past of the animal is represented, and it begins to have an integrated identity, a self. This fusing of past experiences with the present is evidently dependent upon the provision of a cortex in which past happenings are in some way represented.

It is well to remember that this cortical memory is not ever-present in the individual. We are not born with it and it is only as the brain develops, and more complex cortical connections are established, that we begin to have any memory for past events or any sense of identity or self. Before six months of age the baby may recognize or remember faces of individuals with whom it is frequently in contact but the power of retention of these memories is extremely slight so that these impressions are readily overlaid, the old being readily forgotten when new faces take their place. There is apparently little fixation of memories at this stage of individual existence. At a later period kinesthetic memory, the memory for movements, is developed and the child learns to walk. Shortly after one year of age memory for vocalized sounds begins to develop but continues to do so very slowly, the baby requiring very frequent repetitions before any vocal habits are fixed. It is not usually till two or three years of age that cortical memory is functioning completely. Up to that time the individual is conscious, but his flashes of attention are not linked up by memory into a stream of activity and the responses are necessarily isolated. We have before this time no sense of individuality, of identity, so characteristic of our experience. There will of course be awareness but this lacks any continued orientation in time and place. Try as we will we cannot reconstruct the past, we can produce no recollections of events and places before cortical memory made this continued orientation possible. This does not mean that there was no memory of any kind before this period but simply that memory was not functioning as it does at a later period. The behaviourists have shown very clearly that many fears and desires are conditioned very shortly after birth and that they are not really inherent as we oftentimes suppose. The fact that these responses are fixed at a time when our mental life is almost wholly unintegrated explains why so many of these conditioned fears and desires persist and are so hard to get under cortical control. They occupied the stage of consciousness at a time when there were few other impressions to dispute possession with them. Many of these unreasoning fears and dislikes remain with us all our days. Their origin is of course beyond the range of personal recollection and to this extent they might be termed unconscious fears, but as regards our awareness of their presence and influence they are conscious enough. But we should note that the experience of the individual is continuous even though the memory is unable to bridge the gaps in that experience. The fears that are built in by conditioning at a very early period are just as undiscriminating and unproportioned as the shying of a horse at shadows on the road. These fears may be quite unreasonable, as witness some people's dread of dogs as compared to their reactions to other animals potentially much more dangerous. In the same way the fear reaction will be shown by a fiddler crab to the flapping of a cloth in the same degree as it will to the appearance of a fisherman. Subcortical fears differ entirely from cortical fears, which are essentially specific and discriminating. The difference between them is the difference between the fear of the tiger behind the bars of its cage and the fear of him at large. The former may be subcortical and is shown sometimes by young children while the latter is cortical.

The psychoanalyst errs egregiously when he attributes a conditioned fear such as some people's dislike of furry animals to far-away ancestral experience with sabretooth tigers. The blunder is just as bad when he links up the symbolic meaning attached to certain objects with specific race memories. This all implies a continuity of experience which is nowhere in evidence. Biological race memories are unspecific. We have no ready-made response to thunder as a specific stimulus but show the same reaction to all loud unexpected sounds. To suppose that because men for many generations saw phallic significance in some natural object other men may be born with this idea is just as ridiculous as to suppose that men will ever be born knowing the multiplication table. Nothing is truer than the fact that when an individual dies his conscious past passes with him, and the development and integration of a new individual means that the slate of conscious remembrance is wiped quite clean.

It is probably true that, before cortical or conscious memory functions completely, we pass through a twilight period, a time of dim remembrance to which many of our so-called subconscious memories are related. Some of these memories can be revived in certain persons by means of a special technique such as hypnosis. Hypnosis is a state of lessened consciousness and is analogous to the stage of development in which the individual was at the time of occurrence of these revived events. The effectiveness of hypnosis in such cases may be due to this reconstruction of the state of conscious development at the time of the occurrence. There are people who claim that they can remember events in the first year of life but these claims are exceedingly doubtful. It is extremely difficult, and in fact impossible, to separate what we really remember in this way from what we have been told or reminded of by our parents. Theories advanced by certain psychoanalysts that certain postures or actions have reference to "unconscious memories" stretching back even as far as our prenatal existence, have no foundation in fact. Seeing that any specific or individual memories must have a functioning brain as their physical basis such assumptions are not only unwarranted, but ridiculous. Memories, conscious or subconscious, which have any reference to the "self" date back only as far as the emergence of that self as a more or less definitely orientated personality.

This brings us to the question of the importance of that orientation. Is it possible for us to be conscious without any sense of orientation in time and place? It is possible, but this kind of consciousness is not typically human consciousness but would be like the flashes of awareness that the lower animals experience. Even when, as sometimes happens, we wake up from sleep without any memory of where we are, we are not wholly disorientated for we are aware of a "here" and "now"; we know that we are in some place and that it is some time. We do not in such cases lose our sense of personal identity although for a time the breaking of the links of immediate memory has a confusing and even disturbing effect. We can all remember that the return of recollection seems in such circumstances like the opening of a door or the flooding in of light. In such cases when there is a momentary break in memory we are conscious of our surroundings even though they are strange and novel. But we cannot be entirely cut off from environment and remain conscious.

Human consciousness, then, may be described if not defined as a sense of aliveness dependent upon an orientation of ourselves in time and place; this orientation being contributed by our senses. It is cortical memory which provides this orientation of ourselves *as individuals* and this is characteristic of the highest animals. Our sensory equipment consists not only of the traditional five senses—hearing, sight, touch, taste, smell—but includes also our sensations of pain, pressure, movement, position and temperature.

It is important to understand how essential is the contribution of the senses to consciousness. We cannot be conscious without this sensory equipment because without it we should be cut off entirely from our environment. There will therefore be degrees of unconsciousness according as this contribution of the senses is diminished or cut off. Fits of abstraction, absent-mindedness, dozing, hypnotic states, sleep and mild anaesthesia, are states of limited consciousness dependent on the degree to which these sensory contributions to our aliveness are cut off. When we are in a brown study, as we call it, it may be that only hearing is cut off; when we are "gazing into vacancy," or in a deeper fit of abstraction, sight and hearing are both partially in abeyance. When we sleep, sight and hearing and smell are entirely cut off; while touch, pain, pressure, temperature, and organic sensations are partially in abeyance. In anaesthesia we are completely disorientated and in the deepest anaesthesia all proprioceptive sensations and even the deepest organic sensations are entirely cut off.

Interesting confirmation of this view regarding the importance to consciousness of our sensory equipment is given by Foster who refers to the remarkable case of the man who was deaf, dumb, blind in one eye and suffering from general anaesthesia, and who, when he shut the other eye, was immediately asleep. If in some way organic sensations could also have been cut out of the picture then the closing of the eye would have meant unconsciousness.

In passing we may remark that the provision of eyelids makes possible the entire cutting off of the visual stimuli with the exception of some rather indistinct light sensations which apparently play an important part in arousing us from slumber. The lower animals, such as the marsupials, have a muscular mechanism by which the outer ear appendages are definitely closed during sleep. In rabbits and hares the ears are laid back but man and the higher animals have no such mechanism at their command. There may, however, be some differences in adjustment in the inner ear itself which may affect the receipt of auditory stimuli. Evidently the act of listening entails some tension of the tympanum or other adaptations favourable to hearing. Prior to sleep this mechanism may be relaxed, and the total effect of this diminishing of afferent stimulation is to lessen the area of cortical excitation of the brain. Sleep is thus seen to be at the opposite pole to attention which is characterized by a diffused excitation. In preparing for sleep everything possible is done in the direction of diminishing stimulation; the limbs are quiescent, the breathing and heart beat rates are slower, the eyes are closed and there is, in deep sleep, a decided contraction of the pupil which lessens the amount of sensitive surface exposed to the influence of light which might filter in through the lids. This latter circumstance points to the operation of a definite sleep centre whose influence is thus seen to be inhibitory as compared with attention which is a re-enforcement of activity. Monotonous stimuli, under our theory of habituation (see Chapter LII), will assist in the diminution of cortical excitation. Certain portions of the responsive mechanism will be in a state of inhibition, or a refractory phase, in which motor response is inhibited and this is a condition favourable to sleep. We have previously referred to the fact that attention is with difficulty divided; we think of one thing only at a time. If now some indifferent or monotonous stimulus absorbs our attention then cortical excitation is restricted to one limited area and the motor response, if any, is discharged along some well-facilitated path. This restriction of the excited area is evidently a condition favourable to sleep. Hence when we cannot sleep we may count imaginary sheep, not because sheep have particular sporific value but because the monotonous counting operation inhibits other more diffused cortical activity. In fact it is easier to go to sleep when attention is mildly engaged with some monotonous activity than when there is none.

The effect of this inhibition or restriction of cortical activity is strikingly illustrated by Pavlov's experience when engaged in experiments with conditioned reflexes in dogs. For instance, a good conditioned reflex had been obtained in animals by sounding a bell ten seconds prior to the presentation of food, the reflex being the pouring of saliva into the dog's mouth, two or three seconds after the bell sounded. If, now, instead of presenting the food in ten seconds the interval was prolonged to sixty seconds Pavlov found that even the greediest and hungriest dogs went to sleep in the waiting interval, and so soundly that firm prodding had to be resorted to in order to wake the animals up again. The animal would go to sleep just the same if instead of a bell a strong electric shock was given as the initial conditioned stimulus. What evidently happened was that when the bell was sounded the animal's attention was absorbed in taking up the waiting attitude preparatory to receiving the food. All other cortical activity was suspended or inhibited, the conditioned stimulus holding the stage of consciousness, as it were, to the exclusion of everything else. When the waiting interval was prolonged to sixty seconds cortical activity was suspended generally. Attention accompanied the beginning of the reaction but was perforce suspended since in the meantime, before the food appeared, there was nothing to attend to. The contribution of the rest of the senses to consciousness being inhibited cortical excitation was so diminished that sleep resulted. If, however, some other stimulus was interpolated into the waiting period then cortical activity continued and the animal remained awake. A similar effect could be obtained by increasing the intensity of the original stimulus which would have the effect of extending the area of cortical excitation so that the previously facilitated path would be insufficient to discharge the neural energy. The same thing may be observed in human reactions. The preacher of a soporific sermon can effectively arouse his audience by suddenly shouting a sentence or two, or the congregation may avoid the usual accompaniment of a prosy discourse by thinking of other things.

It seems unwise, however, to decide that inhibition and sleep mean exactly the same things. Inhibition of diffused cortical activity is an essential accompaniment of the attentive attitude as in the learning process and at such a time we are surely wide awake. But it is inhibition of cortical activity when there is no relevant stimulus holding the neural stage, so to speak, which causes drowsiness and sleep. Hence we go to sleep over our studies when the subject matter is dry and uninteresting much easier than when attention is taken up with a multitude of changing activities. In short, we use part of the mechanism of attention—the inhibition of widely diffused cortical activity—as one factor in inducing sleep but combine it in association with an irrelevant or indifferent stimulus. Sleep is thus to some extent under voluntary control.

Dreams may best be explained on the basis of a neural overflow of after excitation of the cells of the brain. There is a residue of neural energy not wholly expended in the day's activities and this may sometimes accumulate in sleep and find an outlet in sub-vocalized thought accompanied by the appropriate imagery. The paths of discharge are naturally those which are linked up with the more commonly facilitated paths. Hence our dreams are related to all kinds of motor activities which are motivated by the common self-preservative tendencies. It is sex and fear reactions and motor activities and such-like that are represented so commonly in dream situations. The statement that dreams always represent wish fulfilments is bare assertion and no amount of clever interpretative juggling will serve to bring all dreams under the one rubric. The fact that peripheral sensations and organic sensations are not wholly in abeyance during sleep may help to account for the accumulation of neural energy resulting in cortical excitement. It is when the influence of these is strongest, as just before waking, that we have our most vivid dreams. That there is neural excitement possible during sleep is shown by the fact that it is sometimes strong enough to discharge itself in overt action such as somnambulistic walking or talking.

If now we are convinced of the essential contribution of the sensory equipment to that sense of "aliveness" which we call consciousness, we may get a better idea of what this consciousness means to the lower animals. In the organism without special sense organs consciousness must be a kind of very dim awareness of living contributed wholly by the sense of touch, organic sensations and the sense of movement, temperature, pressure and pain. In simple terms we may say that the animalcule would hardly know it was alive except for such senses as touch and other organic sensations that it possesses. There would indeed be a very dim and indistinct sense of aliveness and any heightening of consciousness would necessarily come through body movement. The constant activity which some of the lower animals display may be the only thing which gives any continuity to their conscious states.

Fundamentally, states of attention do not differ from states of consciousness. Both depend on an active contribution by the senses. We cannot be aware of anything without attending to it in some degree or manner. Even our organic sensations are the objects of our attention. We cannot be conscious without attending to something, however dimly. Attention means the activity of some or all our senses and when we absolutely cease to attend to everything we cease to be conscious. It is needless to say that attention is always directed toward some object while consciousness may be entirely subjective. We have already seen that we can be in a measure our own environment, or to put it in another way, environment is both internal and external. When the state of my digestive organs determines my actions then my stomach is in a sense providing the environmental stimulus while if the cortex initiates the movement then the cortex provides the stimulus.

For convenience sake it would be better to apply the term consciousness to that sense of aliveness that is contributed by the senses in general and to reserve the term "attention" for the more restricted or concentrated phases in which the special senses of sight, hearing, touch, taste, and smell are involved. In the learning process it is the two first named senses that are principally engaged.

It may be necessary to say something regarding the physical basis of consciousness. On the strength of the fact that consciousness tends to be a lesser accompaniment of actions that become automatic by repetition, it is supposed to be connected with resistance at the synapses, the idea being that as resistance to the passage of nerve impulses increases consciousness is also heightened. This theory seems to be tantamount to relegating the cell body to relative insignificance and unduly exalting the synapse, which, after all, is merely a point of contact or transmission between the terminals of nerve processes. We can arrive at a much more plausible working hypothesis if we regard a condition of excitation of the nerve cells as the physiological correlate of consciousness. The greater the degree of excitation and the wider its diffusion the greater the degree of consciousness. When there is a specific or localized area involved and a facilitated path of response then excitation by the stimulus is slight, the neural energy being very quickly discharged. When unusual or striking phenomena present themselves the already facilitated pathways cannot carry off all the neural energy and the strength of the stimulus may in such cases be increased by the tension of the receptor mechanism. Hence there is a wide diffusion of excitation involving large areas of the cortex and as a consequence a greater degree of consciousness. We have already described the acquisition of new motor activities in these terms and this accounts for the greater degree of attention accompanying the first reactions.

The initial effect of a drug such as alcohol is at first to excite and later deaden the nerve cells. Fatigue, too, is accompanied by a loss of neural energy. Under these circumstances resistance at the synaptic junctions may be raised relatively, but coincident with this there is no heightening of consciousness. Chloroform and other anaesthetics surely exert their physiological effect not on the terminal points of dendrons, but on the nerve cell body, the neuron itself. There may be a relative increase of synaptic resistance but this will be due to the lowering of the neuron tone and it is the loss of efficiency in the nerve cell body which brings about the loss of consciousness.

To imagine that consciousness or attention could in some way be a function of synapses would seem to contradict all that we have said of cell sensitivity. We have shown that it is the cells of the external nervous system that are sensitive, and it surely would be strange if we were suddenly, in dealing with the central nervous system, to shift our emphasis from the cell to the point of junction between nerve processes. Undoubtedly synaptic resistance can be lowered by the repeated passage of an impulse along a definite nerve path as in motor habits, but the lessening of consciousness, as we have pointed out, can in such cases be attributed to the lessening of cell excitation.

In one sense, resistance at the synapses may be considered as an accompaniment of consciousness but from our viewpoint it is not its sole or most immediate antecedent. Our position may be clearer if we liken the brain cells to a reservoir into which water may be poured faster than the canals, which ordinarily discharge the flood, can carry it off. We shall suppose that these pipes or canals are the neuraxons and each is provided at its mouth with a bar which corresponds with the resistance at the synapses. The inlet pipes are the various sensory channels and the accumulated flood represents the incoming sensation, the resultant pressure being analogous to the cell excitation which we call consciousness.

Now let us suppose that one channel is opened in response to some phenomenon, let us say that we hear our name called in a very loud tone of voice. It is an unusual experience—there is no already facilitated path of discharge. Neural pressure at once accumulates and under our theory of neural counter-currents the excitation is reflected back to the periphery bringing about a tension of the whole receptive mechanism and thus automatically widening the intake channels. The flood spreads, the neural pressure increases, and the ordinary channels of discharge being inadequate, seeks other levels of discharge. We may carry the analogy a step farther by supposing that once an adequate channel of discharge has been discovered, the bar will be swept away and the channel deepened so that if the same experience recurs over and over again, the neural pressure will very quickly be relieved and consciousness or attention become less and less of an accompaniment. We may suppose that our response takes the form first of a nervous start, a stiffening to attention and a running forward to the spot whence the voice proceeded. If the stimulus is repeated sufficiently often, we will first eliminate from our response the initial start, then our attention will relax, we may walk instead of run, next we may merely answer "What?" and finally make no response, and if attending to something more relevant fail to hear the call at all.

Now undoubtedly in the beginning when the stimulus was fully effective there was heightened resistance at the synapses but this may justly be regarded as much an effect as a cause of the accumulation of neural pressure. In other words the pressure may be proportionate to the amount of intake as well as to the extent or facility of discharge, but the first factor seems to be of primary importance. To speak only of the resistance at the synapses as the sole cause or physical accompaniment of consciousness is to neglect proper reference to the condition of pressure in the reservoir, the nerve cells. Hence we prefer to consider consciousness as being the mental accompaniment of widely diffused excitation of the nerve cells, an excitation contributed by the senses, and heightened by conditions of inadequacy of motor discharge.

CHAPTER LIV

ENJOYMENT AND APPRECIATION

In tracing backward the steps of man's development in behaviour it is necessary perhaps to remind ourselves that man does not live by bread alone; in other words that necessity or biological advantage does not dictate or influence all his conduct. A goodly proportion of our activities is related to the more fundamental drives of sex and self preservation but there are other activities which lie outside these basic motives and yet are very effective motives for conduct. How shall we account for these tendencies, such, for example, as man's aesthetic appreciation of scenes of natural beauty, of the form and hues of flowers and the multicoloured glow of sunsets? Considering the attention which the rare and striking phenomenon excites we may account for the urge which impels man to explore the unknown, but how can we account for the wonder and pleasure which the unusual so often occasions us? Why is it that a feeling of excitement will be pleasurable in relation to some situations and quite the reverse in others?

We have already pointed out that it is to the animal's biological advantage to attend to the extraordinary or unusual stimulus provided that it has at its command distant stimulus receptors and the means of reacting adequately to the situation. Our whole nervous system is keyed up, so to speak, to attend to such phenomena, originally because of the potential threat or advantage which unusual situations implied. As we have seen, the stimulus to which we have become habituated either no longer has power to call forth any response or it may call forth only a limited response. But how is it that pleasure or satisfaction accompanies our responses to some unusual situations and not others?

It is evident that a feeling of dissatisfaction does accompany an inadequate response to a relevant situation, relevant, that is, in the sense of being pertinent to the continued activity of the organism or some part of the organism. Further, we know that the more our response falls short of adequacy in proportion to relevancy the greater the discomfort or dissatisfaction we feel. But we have previously pointed out that the adequacy of the response is also a measure of the potency of the stimulus. The situations to which the animal by racial experience and of necessity has come to respond adequately will continue to call forth a facilitated response. They are what we have designated "prepotent stimuli." But circumstances alter, so that in certain situations the factor of necessity is diminished or disappears, i.e. the relevancy of the situation is lessened. Here again we have a lack of proportion between the relevancy of the situation and the adequacy of the response, only in this case the disproportion is in favour of the response. Just as we found that dissatisfaction accompanied the inadequate response, so conversely satisfaction accrues in those activities in which relevancy is relatively diminished. We may speak of this decrease of relevancy as freedom from necessity or environmental load. It has the effect of providing a mild overflow of neural energy having its issue in a state of diffused but pleasurable excitement of the nerve cells.

Instances of the effect of this freedom from necessity or environmental load are common enough. It would be hard to believe that the hare receives any pleasure from the muscular activity involved in escaping from the hounds yet the same amount of energy expended in gambolling on the green would appear to result in evident enjoyment. The pursuit of game by wild dogs or wolves is almost as serious and grim a matter for the hunters as for the quarry, if, when they are pursuing the game they themselves are driven by hunger or starvation. The only difference is that the quarry is in more imminent and immediate danger. Hunting is in these circumstances a very serious business and very different from the joyous pursuit of a fox by a pack of well-fed hounds. With animals as well as man it is the gains which are made somewhat in excess of bare necessity which give the most joy. What we call pleasure is evidently associated with acts which were originally essential to self preservation in some degree and which by a change of habits or living conditions of the animal have become somehow freed from this load of necessity.

According to the hypothesis put forward in earlier chapters of this book, sex activities were earliest divorced from their original relation to the self-preservative tendency and thus by being set free from necessity occasion the keenest kind of enjoyment. The satisfaction which the rearing of offspring normally brings is also in part due to the performance of acts which once were relevant to the well being of the animal itself but which have largely if not completely lost this significance.

Hunting, in the animal, is an instinctive activity which is of course a built-in habit but in the case of the hound is no longer essential to its self preservation and is entered into with so much more zest on that account. The more strongly built-in the habit is, and the more it can be divorced from necessity, the greater the satisfaction which is attached to its indulgence. This has already been illustrated in respect to sexual activity. The pleasures of love are so much the more heightened because we are no longer driven by necessity to love. The satisfaction of the sexual impulse has become an end in itself.

Keeping this principle in mind we can explain many of the more generalized pleasures and satisfactions. The seeking of shelter by primitive man in caves and cliffs and rocky eminences was enjoined on him by necessity. Such places were for long ages his natural habitat and formed the background of his most satisfactory orientation. Specifically we cannot inherit an interest in rocks and caverns but what we can inherit is a tendency to react strongly to the unusual, because of its promise of potential advantage or potential threat. Hence, the plains dweller may show great interest in a small eminence and the mountaineer in some tiny hill-girt meadow or flat. This interest in the unusual which is an inherent reaction must not of course be confused with the satisfaction which we obtain from our familiar background in natural surroundings. The mountaineer may feel disturbed or dissatisfied if forced to live on a plain and the plainsman may feel that the mountains are harsh and repellent, but this is entirely a matter of individual experience. By a natural process of conditioning we grow to love the places where we have been the happiest. The house we lived in, the garden we loved, the woods we played in, become part of our stimulus patterns and the sight of them will serve as cues to recall our previously experienced happiness.

Man no longer seeks mountains and woods for the advantages of concealment and protection and so is able to respond to association with them with pleasure. Immediately the question of environmental load comes in, his satisfaction is materially lessened. To the man who is forced to make a living by agriculture among rocks and dense woods their beauty conveys a very hazy hint of satisfaction. The bushman in Australia, intent on making a homestead in the forest, regards the disapproval of the nature lover at the ruin wrought by his axe and fire as a most extraordinary and impractical concern. The things that delight his soul are the naked clearings with their promise of fertility and harvest.

In order to give zest to a situation it must in large measure be a situation of our own free choosing. The neural overflow from an over-facilitated response, over-facilitated, that is, in the sense of diminished relevancy, must in such cases be a cortical overflow. Delay in response is an indication of freedom from necessity and so it is not surprising that we find this a frequent feature in pleasurable experiences. We cannot enjoy scenery in hurried glimpses. Such fragmentary experiences merely tantalize us; we must drink them in. We must always have time for enjoyment and the taste must linger on our palates in order to be enjoyed most fully and discriminatingly. Discrimination is secondary when necessity steps in. To the man famishing with thirst, plain water is as good as the finest wine, and to the starved, dry bread is as good as caviare.

It is freedom from the necessity of immediate response which makes our eye and ear and nose—the distant stimulus receptors—the main purveyors of pleasure. The first two senses are the most discriminating. The remembered touch of a vanished hand may not differ much from other touches in the dark, but the sound of the voice that is still can rarely be counterfeited. It is the setting free of the eye and ear from the necessity of standing guard which has made them the chosen instruments of our satisfaction. But should the situation be changed by the injection of some element of danger the pleasure subtly but inevitably decreases. No one really enjoys taking a risk unless he has an onlooker to admire his hardihood, in which circumstances the matter becomes one of self display and assertion which may overshadow the element of risk. No one can really appreciate wild mountain scenery while his foothold is precarious. A foot farther from the edge of the precipice may make an immense amount of difference to our appreciation of the scenery. The element of danger in the situation demands our whole attention to the exclusion of all pleasurable considerations. Under the spur of competition or under the eye of the crowd a man may disregard ordinary risks but usually his enjoyment of the situation will be proportionate to the degree to which attention is absorbed in achievement, to the exclusion of the ideas of risk.

Our interest and pleasure in games of competitive skill are great because usually the situation is free from any element of necessity. The activities are those into which we enter of our own free will and not because we are forced to do so. They are often imitative of those which are extremely relevant from the standpoint of survival or biological advantage. We enjoy the game usually because it is only the game itself which can be lost. It is significant that the freeing of animals from environmental load will predispose them to play. The kitten whose existence is provided for by its parent will indulge in play which has all the appearance of vital purpose but is purely in the nature of make-believe. So the colt kicks up its heels, the young lambs race and butt each other, dogs engage in furious sham battles, while alternate pursuit and flight form the basis of most of the natural play of man or beast. Through make-believe mechanisms the actions are freed from their original purpose and value and come to have meaning and value of their own. Imaginative substitution is of course the basis of the boy's interest in the story of adventure or the girl's absorption in the ardent love romance. They may enjoy all the thrills of conquest without the attendant penalties, risks or obligations.

There is also a more passive manifestation of pleasure which is due to the removal of some worry or pain or the fear of failure, illness or poverty and which is also shown in the satisfaction of some long-thwarted desire.

Summing up the discussion, then, we may say that foremost among the factors essential to a satisfactory or pleasurable activity is the freeing of that activity from the load of necessity. It must be a situation of our own choosing and the delaying of response being the earnest of safety this is frequently a feature in the situation. Even in aesthetic appreciation there is the appeal of the unusual and the striking. Commonness of occurrence undoubtedly robs situations of their due meed of appreciation. It is the picture which shows a rare degree of artistic execution, the muscial composition of unusual melody or tonal combination, the flower of uncommon size, shape or colour, the brilliant sunset, the awesomely plunging waterfall, the lake's unexpected quietude, the silence of the church in the midst of the busy city, the woman of a rare order of form and beauty—these are the things that arrest and thrill us. They call for our attention and yet are entirely free from potential danger or alarm. Drab monotony fails to hold our attention while in other situations jar and discord and clamour have in them some hint of disturbance or danger and hence are reacted to with dissatisfaction.

But just as the cortex gave us more things to fear so it has also given us more things to enjoy. As civilization progresses there is a multiplication of things which are worthy of our attention and which are free from environmental load. The range of pleasurable objects and pursuits is greatly augmented by association and education. Parents are continually calling the child's attention to things which they themselves consider striking or worthy of appreciation, but though education and instruction may increase this interest, response to the unusual is fundamentally the basis of this appreciation.

The wonder and pleasure with which a person of poetic or artistic tastes watches a fiery sunset or a storm-wracked sea seems to be on a very different footing from the interest which the yokel displays when regarding a two-headed calf, but both interests, though far apart, have the same basic origin. At one time in the history of mankind it paid the yokel's forebears to pay attention to the portents of storm and at the same period and stage of human development it paid the poet's ancestors to attend to the appearance of some unusual animal. Nowadays both situations have lost their relevancy from the standpoint of survival value.

The increase of intelligence that a better-developed cortex implies has resulted in a much wider range of choice of interests and pursuits and a consequent increase of objects of pleasure. It is not that the poet and the yokel do not share the same fundamental satisfactions but it is in the range of their interests and enjoyment that they differ most. Within the range of the intelligent man's chosen interests are many things outside the dullard's experience which could only be participated in by the latter at the cost of intense effort at understanding which would rob them of their pleasure. It is in the range and variety of his pleasures and not in their absolute choice that the intelligent man differs from the fool. So the wise man can still retain his interest in the common joys of living, may even rejoice in a somewhat coarsened and primitive sense of humour and be none the less wise.

While considering the pleasurable effect occasioned by the artificial or natural subtraction of relevancy from what was once a racially prepotent situation, it is odd to reflect how often our enjoyment of a verbal or actual situation is connected with the detection of irrelevancy of another person's response to that situation. Our enjoyment of the situation is heightened when the chief actor is unaware of the incongruity of his acts or speech whilst at the same time that irrelevancy is to the onlooker plainly apparent. The same thing is true of many witty remarks and humorous comparisons. The statement that the dissimilarity between a Scotchman and a coconut is that you can get a drink out of a coconut delights us with the real irrelevancy lurking behind an apparently valid and meaningful comparison. The sex story usually gets its point from the fact that the hidden significance of the situation makes the ostensible meaning and application irrelevant in comparison. Thinking over many of the funny stories or episodes with which I am familiar, I realize that their humour consists mainly in using an actually innocuous episode or statement in such a way as to give it a very significant hidden meaning which makes its apparently innocent character or relation entirely incongruous by comparison. It is the element of incongruity, or irrelevancy which makes so many situations humorous. Children's sayings, double meanings, Irish bulls, witty retorts, plays on words, are distinguished alike by this element of incongruity or of irrelevancy by contrast. The detection of incongruity is of course not the only element in our enjoyment of a humorous episode. There must also be an element of unexpectedness, a swift dénouement or an anticlimax involved. The unusual or striking makes its inevitable appeal to our interest and attention, and if this interest is held in suspense, our enjoyment is considerably heightened. Then in addition there must be an element of subtlety in the situation; the joke must not be too obvious or broad. Humour then seems to consist in the main of the detection of unlooked for irrelevancy or incongruity, often disguised under the appearance of aptness, in a situation presented in an unusual way. The more cleverly disguised the incongruity is the more subtle the humour. Herein seems to lie the main differences in grades of humour. The person with a poor sense of this saving grace is sufficiently amused if the situation is merely incongruous on the score of vulgarity, obscenity, blatant stupidity or obvious misconception. The person with a higher sense of humour enjoys the incongruity so much the more if it is well disguised under the appearance of aptness. The stupid yokel and the smug or conceited person share this characteristic in common, that they enjoy only the situation involving the foolish discomfiture of other people. Humour is a saving grace only when it enables us to see that it is in our most serious moments that we are frequently the funniest.

CHAPTER LV

THE CORTEX AND INTELLIGENCE

From time to time references have been made to the cortex as the organ of individual response, the organ whereby the animal may step outside the trodden paths of general biological experience. Anatomically, as we have seen, it provides higher networks of nerve cells and connections into which neural excitation may overflow, if, when a situation is reacted to, neural energy is not wholly discharged along prefacilitated pathways. The animal with very little or no cortex can make very few modifications of response, can learn but little, because it has little to learn with.

In purely psychological terms the highest function of the cortex is to enable the animal to make new adaptations to situations. Throughout this book we have been careful to put the emphasis on the adaptation, the response. It is the adaptive response which is new and not the situation. After all, the spider's environment is much the same as my own, but its responses are entirely different. In thus defining the highest cortical function as capacity for new adaptations we part company with the majority of psychologists whose accepted definition of intelligence is "general mental adaptability to a new situation." It is unwise to lay so much emphasis on the newness of the situation instead of on the adaptive response. In another book[1] this capacity for new adaptations has been condensed, as a definition of intelligence, into "progressive adaptability."

Elsewhere we have pointed out that the cortex plays a dual rôle in behaviour. It may not only initiate movements working through its connections with the lower motor neurons, but to some measure by its command over the voluntary muscles it can control movements. But its supremacy is not wholly established; even in man there is some instinctive behaviour which evidently finds its neural basis in prefacilitated paths at some lower or sub-cortical level. As examples of this we have mentioned certain responses in the way of fear reactions etc. There are some reactions which are so fundamental that there can be no delayed response. In such cases it takes the cortex some time to swing into action. The nervous man cannot restrain the involuntary start of fear but he can control the additional response of running away. In the same way though by cortical control we cannot prevent ourselves from feeling angry, we can restrain the blow. The feelings of shame or disgust which have their neural basis in the thalamus are not immediately under cortical control but the cortex, if given time, can effect a great change in our emotional state by helping to bring about a process of mental habituation to the situation. The cortex can dictate movements which put us in the position of repeating the occurrence, and as we have seen in Chapter LII our response to the usual is attended with less and less neural excitation and overflow. Getting used to a situation is a process of repetition by which the pathways become facilitated and a more adequate response is found. Part of this increased adequacy of response may take the form of a verbal recognition of the situation. In common terms we say that we persuade or tell ourselves that the situation represents an unavoidable state of affairs, that we may as well get used to it, or that there is nothing to be done about it; in short, that it is irrelevant and therefore not to be attended to. It is wonderful how many situations, initially embarrassing, terrifying, or shocking there are, that by means of cortical intervention may be reacted to eventually without these emotional effects. We can get used to almost anything if we have the will to do so—but this is by no means an immediate happening. The cortex has no direct control over the lower centres but only through the voluntary muscles and this is a process which takes time and repetition. By practice we can learn to control movements of single muscles in the body and by practice in a somewhat similar way, we can learn to control in great measure our instinctive or lower-level responses.

---

[1] *Temperament and Race*, by S. D. Porteus and M. E. Babcock.

Bravery may be inherent or it may be a matter of habit. Conversely, many of the actions of insanity are learned or imitative conduct.

We do not fear because we tremble as the James-Lange theory postulated, but these actions may be regarded as parts of the one process. Both may be due to an excess of neural energy which finds no adequate path of discharge. Both the fear and the trembling may be diminished or removed by the substitution of a more definite or specialized motor response, as advancing or running away. Part of the diffused neural excitation is in this way taken up and discharged in some other less overt way, as by thinking that there is no danger or that our fellows will see our cowardly trembling, or some other thought response.

In all of this discussion of the functions of the cortex we may seem to have dwelt unduly on motor responses, leaving out of consideration much of mental behaviour that seems to be altogether apart from the purely physical response. Though behaviourists in some respects have gone far beyond their facts and have contradicted common experience, they seem to have made a very great advance in their theory that thought is vocalized or sub-vocalized. They believe that we always think in words. Now leaving out of consideration the evidently debatable question as to whether thought is exclusively of this nature, we may say that it is almost invariably sub-vocalized or vocalized, i.e. that it is a motor response. Some of us may find it possible to think in images instead of words and the deaf and dumb person naturally has no words at his command and yet may think; still we believe that for all practical purposes we may regard thought as being in the category of motor responses. A very large percentage of our thinking is of this character and for some of us our vocal habits are so established that though it might be possible to think without words we never do so. A habit of vocal expression is of course not confined to man but has far and away its greatest development in him.

The ability to convey ideas by the use of vocal symbols constituted one of those distinctive advances in function of which only an animal, cortically endowed as Man is, could be capable. It was perhaps the most critical of all advances in Man's phylogenetic progress, since it definitely established his supremacy over the rest of the animal kingdom. Before considering any of the theories which seek to explain the origin of words let us glance at the conditions under which language itself was developed, and which gave it such pre-eminent importance.

We have considered elsewhere the value of an arboreal habit to Man's ancestors in freeing them from the immediate severities of the struggle for existence and giving them leisure and opportunity for that experimentation and choice of action which was to constitute the special distinction of the human cortex. This freedom from competitive stress was in its way as important as the provision of distant sense receptors and was indeed the immediate precursor of the superseding of smell as a warning and guiding sense.

One of the important effects then of life in the trees was that the arboreal animal, being freed from the necessity of ensuring survival by specializations of bodily equipment either for flight or defence, was enabled to retain its biological plasticity and could thus avail itself of the evolutionary impetus that this change of habit afforded. There was also the fortunate circumstance that the proto-human stock was already insectivorous and fruit-eating. The necessity for wide ranging of the forest in search of sustenance created a demand for highly co-ordinated muscular movements. If there had not been a premium set on this new kind of activity, the freedom from environmental stress might have resulted in the evolutionary stagnation which overtook most of the purely herbivorous tree-clinging stock.

But having exploited the advantages of arboreal life to the full, Man's remote progenitors had to descend in order to make any further advance. Life on the ground offered obvious advantages to the animal with sufficient cortex to be able to avail itself of them, and we must assume that Man had during arboreal existence developed that cortex. But had he remained a tree climber and clinger he would hardly have become *Homo faber*, Man the tool user, as Bergson calls him. Some of the higher apes have been shown by recent experiment to have some insight into the use of sticks as tools but the problem situations in which they have shown this aptitude are humanly devised and are likely to be extremely rare in natural surroundings. Reaching for food through the bars of a cage with a stick and piling up boxes to obtain food suspended out of ordinary reach are of course artificial situations, and in any case are problems only to be solved on the ground. The effective use of a stick as a club or a lever requires a firmer stance than is obtainable in the tree-tops. Stones as missiles can also best be used where they can best be obtained—on the ground. With the lengthening of the period of infantile helplessness—a condition coincident apparently with a state of ultimate high development in general—life on solid earth would apparently provide much better insurance against risk than would life in the branches. Especially would this be the case if the human stock had already proceeded any great distance towards bodily nakedness. The young would be able to help themselves but little by clinging to their parents. The attainment of the erect posture and plantigrade locomotion would indicate that descent occurred at a very early period in Man's phylogenetic story otherwise he would have become as the ape, and psychologically speaking, between them there is a great gulf fixed.

As to the circumstances that led to Man's descent from the trees we can only speculate. It may have been that climatic changes occurred which made forests sparser and sustenance from ground fruits, berries, and insects easier, and so Man's primitive stock was forced down as was the case with the African Baboons. On the other hand it may have been that the proto-human became too heavy for arboreal life. A more directly psychological theory is, however, at least worth entertaining; he may have descended from the trees because he had developed a cortex which was capable of taking advantage of the facilities that life on the ground afforded. Whatever the cause, one fact is certain, and that is that immediately he did descend his risks increased immensely. His natural enemies had decreased neither in ferocity nor means of offence. Without the means of rapid flight our early ancestors must have depended for protection largely on the concealment afforded by thick brush or cave shelters. These were exactly the conditions under which smell as a monitory and guiding sense would have been most useful to him, but as we have seen, arboreal life had resulted in the dethronement of the olfactory organ as an important receptor. Distant vision and hearing had attained, it is true, an enhanced value but under these circumstances they were inadequate as protection against the carnivores who could trail a man by scent to any lair which he might have chosen.

It is doubtful whether a ground-ranging habit would have been more than a temporary and dangerous experiment had not Man, ill equipped for offence or flight, fallen back upon the expedient of the defenceless—the gregarious habit. But we must remember that an animal cortically well endowed would not be forced to rely upon mere herding together for survival; that in short, his gregariousness would have been of a different kind from that of the lower animals. Gregariousness in Man would naturally result in concerted action at a level impossible, say, to the baboon. How could this concerted action best be brought about?

It is obvious that if Man had developed only a simple gesture language this means of communication would only have been useful in the direction of group action if the communicants were face to face. An army of men suddenly stricken deaf to vocal commands would be a helpless rabble if operating in thick brush or darkness. The development of vocal language evidently came about through the necessity for the leader of the group or herd to make imperative or guiding sounds, meaning being attached to them by appropriate gestures made when visual communication was possible. The diffusion of cortical activity in times of excitement would result in vocalization in association with bodily movements so that the opportunity for it to become a conditioned response would be provided.

The origin of words, or why certain sounds should have particular meanings, is the subject of various theories. There is, for example, the imitative theory that assumes the word to be a vocal representation of the sound made by the animal or object and thus to become the symbol or name of the object. This theory when extended somewhat, becomes the onomatopœic which seeks to make imitative association the basis of origin of very many words.

Undoubtedly this derivation of words by "clang" is one means by which language has been enriched. There is also the theory that Man's own instinctive cries became modified into speech and this seems allied to the "interjectional" theory which postulates that sounds associated with different emotions form the basis of words. More recently there has been an attempt, mainly by Paget, to derive speech directly from gestures, the theory being that ideas were first communicated by a generalized gesture in which the tongue and lips participated by imitating the hand and arm movements. The sounds made under these circumstances were retained after the rest of the gesture was eliminated, Man as a craftsman requiring his hands and arms for other purposes than gesturing. This hypothesis of considering articulatory movements as the lineal descendants of pantomimic gestures is interesting and to a certain extent feasible, but we must beware of evoking it too generally. There is no reason why the tongue and lip movements should imitate the hand and arm movements. Due to their essentially different form and musculature they are much more likely to have a distinctive character all their own.

Further, in considering any theory of the origin of words as vocal symbols of ideas, we must not neglect the influence of chance association. Man, psychologically speaking, is extremely subject to whim and caprice, and so chance associations between sound and object are bound to be made. If the leader of the tribe should chance to designate an object by a sound, the latter may arbitrarily become fixed as the symbol. In our own time we have many instances of the widespread adoption of words or slang phrases which in themselves are practically meaningless.

To these theories, all of which should possibly be evoked as playing a part in the origin of words, we would add another which would seem to be more directly psychophysical or psychological. This theory assumes that the mood of the speaker, whether of anger or pleasure, has apparently come to have as part of its motor expression, certain muscular sets either of tension or relaxation, which involve the musculature of the vocal mechanism. In accordance with the idea of cortical diffusion, vocalization tends to be part of this generalized activity. For example, we all know the tendency to set the teeth and clamp the jaws and to contract the muscles of the neck when enraged or determined. The sounds that can most readily be made under these circumstances would therefore tend to be tinged, so to speak, with the mood of the speaker. In other words they would have an appropriateness, not because they have any meaning inherent in themselves, but simply because they are the sounds easiest made under the circumstances. The sounds that can best be made with the teeth almost closed are "r," "s," "t," and with a minimum of movement of jaws and lips, hard "c," or "k." The theory here put forth is that the muscular appropriateness of these sounds will tend to result in a tacit recognition by us of their appropriateness in meaning. Hence they will become the basis, in different combination, of words which signify violent or intensive reactions. Conversely, sounds which allow of maximum of movement or relaxation of the jaws and lips, such as "l" or "p," would hardly be used as the dominant or initial sounds of words made in such moods of intensity. As language became elaborated the words which would survive in common speech would have these characteristics, their appropriateness would be tacitly recognized, and so the language of intensity would grow by this process of psychological accretions.

In order to test this theory the writer is at present engaged in a study of common speech. From an ordinary dictionary some 800 words indicating intensity were culled and this list was submitted to a number of judges who selected the words which to them had the greatest intensity of meaning. The results show that in the 100 most "violent" words thus determined, the sounds represented by "r," "s," and "t" were most commonly present. As first, second or third sounds, "r" was present in 64 per cent.; "s," 37 per cent.; "t," 28 per cent.; and "k," 23 per cent. of the words. The sound of "l" was present in 30 per cent. of the words, but usually in association with other consonants from which it borrowed its force. Incidentally it was found that women to a certain extent speak a somewhat different language of intensity from men. They tend to consider words "violent" which have a definite relation to death, they have a truer sense of word values, and are much more conservative than men. The men are fond of the newer, or slang words, so that the language of intensity is still growing, mainly by masculine additions.

From these results it would seem that there is a definite place for this "motor-intellectual" theory of the origin of words among the hypotheses which seek to account for the development of language.

Whether vocalized or sub-vocalized, the use of speech must result in a very large portion of the brain being concerned in this most important motor function. When we add to our repertoire of vocal speech the writing and reading habits and thus bring the eye and the hand as well as the ear into relation with the speech mechanism, we surely have need of very many more cortical neural connections.

With these newly acquired abilities for visual as well as vocal speech within the scope of his learning capacity, Man, as a species, has fortified himself in his dominance over the rest of the animal kingdom in a unique way. He may now add to his physical inheritance a social inheritance as well. In other words, instead of waiting for the slow and laborious business of building variations of structure into the warp and woof of his physical being before his behaviour can change, he can acquire for himself all that men before him have gained as the fruit of their labours. The history of evolution has been that of dominance of the earth by some phylum followed by its eclipse due to the more or less sudden advance of some other phylum through some superiority in adaptive mechanism. Man's attainment of speech and his invention of writing and reading have meant a permanent accumulation of individual gains and experience. These constitute now the social inheritance of the last-born individual so that as far as competition is concerned, the other phyla are hopelessly outdistanced. The only possibility of failure for Man is through extinction or else through progressive and complete deterioration. So long as there is a normal man alive he will continue to be lord of the earth. There are many, however, who believe that progressive deterioration will be Man's lot on earth and they point to birth control, the preservation of the unfit, the increase in insanity and feeble-mindedness, the wastage of warfare, individual selfishness and racial heedlessness as the unmistakable signs of the times, the handwriting on the wall. But if Man's cortex is ever displaced or superseded as the ruling factor on earth it will be only by a better cortex. Of course extinction may be the end of Man as it has been that of so many phyla before him and he may fall before some ubiquitous bug or subtle race poison, leaving the evolutionary stage free for the rise of some new phylum to dominance. But provided that Man's mere survival is assured then by the accumulations of social inheritance he will continue to hold his dominant place.

Though we have said that with the birth of a new individual the slate of individual remembrance is wiped clean, we must realize that education very soon begins to write on it. Our use of the slate as an analogy must not, however, be taken to mean that we believe in the old idea of the associationists, who held that each individual was at birth like a "tabula rasa" upon which environment and education may write what they will. Despite the fact that some of the behaviourists have revived the notion and given it their support the situation as regards mental inheritance is entirely different. Education, or environment, writes on each slate the lessons of social inheritance but some slates are much better as writing material than others. Some have such a texture that they will take indelible markings, others may take only a very soft and quickly vanishing impression, while others again will not take any mark at all. The behaviourist who claims that he could take a child of any parentage, and given a world of his own choosing in which to bring that child up, could make him into a successful member of any learned profession, is disregarding the known facts. Almost one hundred years of intensive educational effort with defectives involving the use of all kinds of ingenious systems of teaching methods have proved conclusively that, intellectually speaking, whatever useful things you may make out of a sow's ear, a silk purse is not one of them. In some of these cases the mental defect has been detected early in life and all the ordinary and many extraordinary educational measures have been taken to obviate it but with pitiably small results. Watson himself would except the mental defective from his statement of the possibilities of education and environment. But it is now well known that mental defect is a matter of degree and that there are all gradations of deficiency from idiocy and mental dullness to normality. Hence Watson would need to except from his claim the mentally dull as well as the grossly defective and once having made these exceptions his initial claim loses all its force.

On the other hand, equally extravagant claims have been made concerning the importance of heredity. Feeble-mindedness is undoubtedly transmissible but not to the extent that some investigators have claimed. Twenty-five per cent. would probably be a conservative estimate of the percentage of directly transmitted feeble-mindedness—that is to say, probably twenty-five per cent. of mental defectives confined in institutions have one or both parents feeble-minded. By using guess work and questionable assumptions this estimate may be largely increased. One very famous study began its story of the transmission of mental defect by the diagnosis of feeble-mindedness in a girl who lived a hundred and fifty years ago and of whom so little is known that even her name has been lost to us. It is obvious that long range diagnosis of this kind is futile, and the study itself was made at a time of very uncertain mental diagnostic standards. The first essential in such investigations is not the making of a mental diagnosis but the publishing of the evidence upon which the diagnosis is made. What are the known facts upon which the mental estimate is founded and how have they been gathered?

Leaving out of consideration such studies we may say that probably sixty per cent. of the feeble-minded come from stock which has more than the average share of neuropathic taint in its heredity. This means that, while twenty-five per cent. of mental defect is directly inherited, in a considerably larger percentage feeble-mindedness and other mental abnormalities are represented on the family tree of the defective in more than the average degree. But though their numerical estimates as to the degree of inheritance may differ, there is little or no disagreement among authorities as to the fact of its importance in the causation of amentia.

Similarly, to assert with regard to instincts and instinctive tendencies that there are no such things is to fly in the face of observable facts. It is true that the number of such tendencies may be grossly exaggerated by some writers and the whole subject of instincts made needlessly confused. But to substitute the term unlearned reactions for instincts does not advance us greatly along the path of understanding. It is also true that individually built-up habits in Man tend to replace the ancestrally built-in reactions but they have not wholly done so. Instinctive tendencies may still be of importance. However, to attempt to gainsay the admitted over-statements of behaviourists is to tilt a lance at windmills that are rickety and unbalanced and will fall of their own accord and are in any case of no importance either fallen or upright. It is quite safe to assume that there are such things as mental traits and aptitudes and that they are subject in some degree to inheritance.

Perhaps some further light on the highest functions of the cortex might be gained by a brief consideration of the behaviour of those individuals in whom to some degree the cortex is underdeveloped. The actions of the feeble-minded may be of more interest to us at present than the question of their heredity.

The first question to be answered is whether it can be shown that there is a diminished cortex in the mental defective. All of the books on mental deficiency show photographic plates of sections from the cortex of the brains of feeble-minded. These indicate that the absolute depth of the cortex is less in comparison with normals and this deficiency in depth is accompanied by a decrease in the number of nerve cells and connections, an irregularity in their disposition, and imperfections in their typical forms. Generally speaking we may accept these differences as fairly valid. Unfortunately even the most careful investigators rarely give the absolute capacities of the brains that are being compared. There is no indication as to whether the brains are of comparable size. The brain of the normal person may be larger than usual or the imbecile brain selected may belong to the microcephalic or extremely small-headed type. In such cases differences in cortical depth might naturally be expected. Indeed we could find just as striking differences in actual depth of cortex between the brains of defectives of different types.

There may, however, be something to be discovered by comparison of the size of the brains of feeble-minded as calculated from the head measurements. If we consider the feeble-minded socially, that is, according to their behaviour, we find them divided into three types. The "pure" feeble-minded, as we might call them, constitute about sixty per cent. of an institution population and considering of course their narrow range of abilities, are well adjusted to their environment. Within that range their behaviour does not differ so markedly from that of children of lesser age. Defectives of the second type differ from the well-adjusted group in being far more aggressive and active in temperament so that they exhibit delinquent or anti-social tendencies. These constitute about twenty per cent. of the general body of feeble-minded. The third group consists of individuals whose mental level is lower than normal but who exhibit irregularities and abnormalities of behaviour. These we call the psychopathic type and they in some respects resemble the insane.

Confining our attention to the common type of defective, those whose chief difference from the normal is a limited range of abilities, we find that these depart markedly from the normal in head measurements also and consequently in absolute brain capacity. For a group of 131 feeble-minded boys whose intelligence quotient was so low as to mark them down as institution cases, the brain capacity as calculated from the head measurements was 1,250 c.c. These averaged 14 years of age, and as the normal brain volume is about 100 c.c. in excess of their capacity, their deficiency was equivalent to about six and a half years' total growth in brain capacity at this age. Another group of 56 boys of somewhat higher intelligence had an average brain capacity of 1,273 c.c. which represents a deficiency equal to about five years' total growth. The differences between the normal and the delinquent and psychopathic groups were not so marked but there was still a significant deficiency in brain capacity. Hence the fact that the feeble-minded possess on the average smaller brains than the normal is indisputable. There are of course among them some remarkably large-headed cases such as the hydrocephalic but the excess in size is due to fluid and not brains. Others may also have large heads but their brains have an excess of non-nervous supporting tissue called neuroglia and are hence poorly organized for functioning.

The most striking characteristic of persons who are deficient in cortical development is their childish behaviour as shown by attitudes and habits and opinions which are similar to those of children much younger than themselves. This permanent immaturity is betrayed in various ways. There is frequently an extreme suggestibility in matters of belief, an acceptance without question of things as they appear to be. For example, they can be made to continue a belief in the Santa Claus myth right up to an adult age. They rarely question motives or attempt to look below the surface so that any plausible appeal or suggestion is readily accepted. On account of this suggestibility they are extremely submissive to authority so that an adult defective will give his best in the way of hard, monotonous labour for a couple of cents a week. Their wants, too, are childish and simple and their ambitions equally puerile.

An inordinate vanity is also a very frequent feature in the defective's make-up. It may take the form of foolish display, a bedecking of themselves with ribbons or make-believe medals. This trait is by no means confined to the defectives as witness the parades of some fraternal orders. In fairness to the latter, however, it should be said that while their members descend to this level several times a year, it is the defective's daily habit.

Another important feature in the moron's personality is his entire lack of insight with regard to his own actions. It never seems to occur to the fool that he is one. His loud, easily excited laughter, his parrot-like repetition of other people's maxims, his obtrusive vanity, his foolish suggestibility, never seem to come before the judgment bar of self examination. He is usually self satisfied but while there is obtuseness to any real indignity there is an altogether disproportionate reaction to slight or fancied injuries.

A lack of any real sense of humour also distinguishes the defective. His appreciation of wit grows rather than diminishes with the repetition of the simple joke. The comparatively few nerve paths at higher levels available in the defective's brain become decidedly over-facilitated so that vain repetition is habitual with the feeble-minded. They can sing the same songs, hear the same stories, perform the same actions over and over again with evident satisfaction to themselves—another childish characteristic. This over-facilitation undoubtedly may serve to explain the apparent persistence of defectives in some monotonous task. It is not that they have an end clearly in sight but the very repetition gives them satisfaction. Indeed, so much of their behaviour is freed from any environmental load that "as happy as a half-wit" would be a very apt comparison.

Perhaps if we were searching for a summation of the mental defective's typical behaviour, we would find it in the statement that to the feeble-minded much of the ordinary person's environment is entirely irrelevant. Though he has a sensory equipment which by experiment has been shown to be hardly less sensitive than that of the normal person to environmental stimuli, he is like the goldfish in the bowl in that so much of his surroundings lacks meaning to him. Within their range his responses are adequate enough but they do not go far enough. His interests are narrow and the finer shades of feeling, appreciation and expression are lost to him. He lives eternally on the fringe of things and whole hinterlands of deeper experience are unknown to him. Lacking adequate means of response he appears blind and deaf to much that forms the food for Man's higher life. He has not brains enough to realize that he is a failure and to be dissatisfied with himself. If he were really cognizant of his own weaknesses it would be an indication of some ability to realize a somewhat complex situation.

But it may be objected that suggestibility, ostentation and self display, ill-founded self esteem, a shallow, sterile humour, a lack of sense of the fitness of things and a narrow range of relevant interests are defects shared in not only by the defective but by rather stupid normal people and ill-trained children. This is undoubtedly true but in the defective these traits are concentrated and unobscured by other outstanding qualities of merit. If these are the defects of immaturity we may ask whether the feeble-minded represent a stage of development through which the human race has passed. This must be answered in the negative for though primitive Man possesses many of these childish or moronic characteristics he acquires in addition other abilities quite beyond the range of capacity of children of any race. In his human social relations he shares the traits of the defective but in his response to his physical environment he exhibits an acuity of judgment which is the wonder and envy of the civilized white man.

In all of our public concern about the proportion of dull and defective people in the community and the discussion of various eugenic measures aimed at lessening their numbers it has not apparently occurred to anyone that from the social point of view it is the frequency of feeble-minded traits in the behaviour of ordinary people at large that is of far more importance than their concentration in the persons of a few hundred thousand defectives in the community. If the picture that we have drawn of the defective is a true social characterization then we must assume that the exhibition of such traits as he possesses indicates, above all things, inferior cortical functioning. In plain terms the more our general social behaviour betrays these fatal flaws, the more immature is our national or racial development; the more satisfied we are to accept this behaviour or let it pass the less hope there is for our future.

In thus laying stress on the social values of the highest cortical functions we are not unmindful that learning capacity is also decidedly limited in the defective. Abstract thinking, the ability to deal readily with the symbols involved in learning, is not within the range of the feeble-minded person's achievement. It is usually in childhood when social defects are not of such importance that this lack is apparent and it is frequently through educational disabilities that attention is first called to the mental inadequacy of the individual. Because it happens to be the first observed symptom it has received altogether disproportionate stress in the diagnosis of mental defect.

INDEX

Action,
  automatic, 224.
  of paradox, 199.
Adaptation,
  dark and light, 322.
  for functioning, 308.
  to environment, 303.
  protective, 267.
Adrenal system, 240.
Afferent fibres, 133.
After excitement, 319.
After images, 315, 321.
Agonists, 196.
Amoeba proteus, 292.
  behaviour, 289, 297.
  food taking reactions, 292.
Anguis fragilis,
  vision and hearing of, 53, 54, 264.
Animals,
  armour plated, 67.
  saltatory, 230.
  sedentary, 36.
  thermostatic and thermovariant, 361.
Antagonists, 198.
Arboreal life, 89, 407.
  use of hand in, 155.
Association areas, 92.
Asynergia, 214.
Attention, 317.
  and consciousness, 392.
  in lower animals, 331.
Autonomic system, 239.
  function, 245.
Awareness,
  of body, 150.
  of fingers and toes, 160, 161.
  of hand, 155.
  of individuality, 285.
  of snout region, 89, 154.

Baillarger, 70.
Bats, voice of, 247.
Behaviour,
  of amoeba, 289.
Behaviour,
  animal, 54.
  instinctive, 360.
  integration, 307.
  patterns, 299, 304.
  and protective adaptation, 18.
Biological advantage,
  of reproduction, 293.
Blindness,
  colour, 282, 309.
  cortical, 268.
Brain,
  of *Cercopithecus*, 105, 111.
  of *Dasycercus*, 98, 110.
  of feebleminded, 416.
  of *Galago*, 102, 111.
  of *Hylomys*, 101, 110.
  of *Phascolarctus*, 103, 111.
  of porpoise, 65.
  of *Pseudochirus*, 102, 111.
  size in animals, 64.
  surface folding, 68.
  of whale, 65.
Broca, 80.

Campbell, 82
Capsule, internal, 175.
Causalgia, 145.
Cells,
  Betz, 175.
  chromaffin, 240.
  intercalated, 5, 57.
  muscle, 4, 41.
  musculo-epithelial, 2.
  pre-oral and post-oral nerve, 26.
  pyramidal, 180.
Cerebellum,
  lesions, 208.
  origin, 192, 209.
  pathways of, 212.
Cerebral hemispheres,
  development, 58.
Choice,
  as cortical function, 300, 354.

Climate, importance, 362.
Colour vision, 281, 309.
Commissures,
  in marsupials, 114.
  dorsal and ventral, 113.
Conditioned response, 118, 268, 376.
Conduct, nature of, 285.
Consciousness, 382.
  and attention, 384, 393.
  definition, 388.
  flow of, 385.
  and synaptic resistance, 393.
Convolutions,
  importance, 68, 69.
  pattern, 70.
Corona radiata, 175.
Corpora quadrigemina, 261.
Corpus callosum, 116, 118.
Corpus striatum, 185.
Cortex, ascendency of, 326, 405.
  and automatic action, 225.
  and control of limbs, 229.
  definition of, 59.
  and enjoyment, 405.
  frontal area, 286.
  kinaesthetic area of, 156.
  motor, 169.
  motor area, 344.
  (*see* also Pallium).
Cortical,
  awareness, 162.
  excitation, 393.
  fears, 386.
  localization, 81.
Cortico-spinal tract,
  (*see* pyramidal tract).
Cytoclesis, 31.
  of sensory and motor ganglia, 44.

Dark, fear of, 274.
Dasycercus cristicauda, 98, 114.
D'Azyr, 72.
Deadness, 250.
  cortical, 253.
Decussation,
  of optic nerve fibres, 279.
  of pyramids, 181, 367.
  sensory, 133.
  value of, 369.
Dendrons, 41.
Distant sense receptors, 335.
  importance of, 341, 354.
Dreams, theory of, 391.

Elberfeld horses, 266.
Emotion,
  advantages of, 326.
  physical signs, 318.
Environment,
  and behaviour, 16.
  and education, 413.
  internal, 299.
Epilepsy,
  Jacksonian, 81.
Excitement,
  motor accompaniments, 317.
  value of, 320.
External ear,
  form of, 258.
Eyelids, need of, 61.
Eyes,
  dark adapted, 269.
  development of, 29, 44
  inverted and non-inverted, 34.
  light adapted, 273.

Facilitation, 301, 314.
Familiar background, 359.
Fear reactions, 327, 333, 380, 406.
  conditioned, 339.
Feeblemindedness,
  characteristics of, 417.
  transmission, 414
Feigning death, 267.
Fetichisms, 320.
Fixators, 201.
Fleurens, 78.
Flight of colours, 325.
Fornix, 116.
Fovea centralis, 308.
Foster, 389.
Frog, hearing of, 54.
Frontal Area, 286.

Gait of animals, 230.
Galago crassicauda, 102.
Gall, 77, 208, 211.
Ganglia,
  basal, in lower vertebrates, 58.
  posterior root, 124.
  sensory and motor, 45.
  sympathetic, 241.
Gaskell, 27.
Gennari, 71.
Germ plasm,
  continuity, 302.
  plasticity, 303.
Gregariousness in man, 409.

Habituation, 323, 373.
Hand, importance of, 89, 147, 155.
Head, Henry, 121, 140, 159, 162.
Head measurements,
  of defectives, 416.
Hearing,
  mechanism of, 248.
  range of stimuli, 247.
Hemiplegia, 136, 170.
Hering theory, 309.
Herrick, 289, 343.
Holmes, Gordon, 140.
Humour,
  basis, 402.
  sense in defectives, 418.
Hunter, 76.
Hunting, 398.
Hydra, 2.
Hylomys suillia, 101, 114.
Hyperacusis, functional, 258.

Inheritance,
  of acquired characteristics, 303, 343.
  of mental defect, 414.
  of specific responses, 305.
Inhibition,
  cortical, 337.
  in conditioned response, 390.
  and sleep, 391.
Instinctive reactions, 301.
  in man, 405.
  self-preservative, 346.
Intelligence,
  definition, 404.
  and interests, 402.
Interest in unusual, 398.
Invertebrates,
  compound eyes, 34.
  nervous system of, 25.
  reflexes in, 126.

Jackson, Hughlings, 81, 175.
Jacobson's organ, 87, 107.
James-Lange theory, 406.

Kappers, Ariens, 43, 75.
Koala, brain of, 103.
Kohler, 331, 372.

Labyrinthine system, 190, 227.
  nystagmus, 193.
Lachrymal duct, 95.
Ladd-Franklin theory, 309.
Lamarck, 18.
Langley, 239.
Learning process, 316.
Lemur, brain of, 104.
Lewes, 79.
Limax agrestis, 53.
Locomotion, neural mechanism, 366.
Luminosity, appreciation of, 264, 281.

Macula lutea, 281.
Magendie, 12.
Magnus, Rudolph, 228, 229.
Mammals,
  hair of, 94.
  smooth-brained, 69.
Marsupials, commissures in, 114.
Medial fillet, 132.
Medulla oblongata, 59.
Memory,
  and after images, 323.
  biological or racial, 301.
  of cells of external nervous system, 315.
  of central nervous system, 316.
  cortical, 385.
Mental alienation, 288.
Mercier, Charles, 288.
Mobility,
  proprioceptive impulses, 367.
  value of, 357.
Motives, human and animal, 298.
Motor nerves, 124, 233.
Movement,
  appreciation of, 265.
  purpose, 291.
Muscles,
  deltoid, 204.
  flexor carpi ulnaris, 201.
  and movements, 167.
  refractory phase, 315.
  trapezius, 205.

Neo-cerebellum, 213.
Neo-thalamus, 218.
Neo-striatum, 218.
Nerves,
  median, 332.
  motor, 174, 233.
  optic, 270.
  sensory and motor, 12.
Nervous system,
  external and internal, 15, 310.
  invertebrate, 25.
  vertebrate, 28.
Nest building, 347.

Neural,
  counter-currents, 332, 338, 381
  energy unexpended, 381
  groove, 6.
Neuraxons, 58, 124.
  in internal capsule, 175.
Neurobiotaxis, 44.
Neuron,
  highest sensory, 135.
  lower motor, 233.
  lowest sensory, 125.
  second sensory, 128.
  upper motor, 172, 178.
Nostril, form of, 96.
Nucleus,
  cuneatus, 133.
  gracilis, 133.
Nystagmus cerebellar, 214.
  labyrinthine, 193.

Olfactory sense, 88.
  diminution of cortex of, 91.
  in wet-nosed animals, 96.
Optic tracts, 279.
Orientation through senses, 387.
Otolithic organ, 190.
Over-facilitation, 338.
Over-production, advantage of, 295, 358.

Paget, 410.
Pain, 129, 130.
Paleo-cerebellum, 210.
Paleo-striatum, 218.
Paleo-thalamus, 218.
Pallium,
  development, 58.
  function, 186.
  olfactory, 85.
  size and surface, 68.
Paralysis,
  agitans, 188.
  hypoglossal, 47.
  of trapezius muscle, 206.
  upper motor neuron, 136, 170.
Para-sympathetic system, 244.
  action of, 245.
Parkinson syndrome, 188.
Pavlov, 390.
Pfungst, 266.
Phantom limb, 162.
Phascolarctus cinereus, 103, 115.
Photopic vision, 272.
Photostatic system, 192, 260.
Phrenology, 79.
Piccolominus, Archangelus, 59.
Placodes, 28, 37, 44.
  olfactory, 86.
Platypus, 154.
Pons Varolii, 211.
Proprioceptive system, 190.
  decussation, 370.
  informative impulses, 367.
  pathways, 209.
Pseudochirus laniginosus, 102, 111.
Psycho-analysis, 386.
Pyramidal tract, 180, 183.
Pyriform lobe, 98.

Race,
  characteristics and climate, 363.
  preservative instinct, 344.
Reactions,
  anticipatory, 327, 334.
  pecking, 331
  righting, 228.
  time, 311.
Red monkey,
  brain of, 105.
Red nucleus, 194.
Reflex,
  complexity of, 304.
  and limb posture, 227
  patellar, 337.
  pupillary, 263, 324.
  sneezing, 171.
  spinal, 126, 216.
  suckling, 45.
  yawning, 172.
Relevancy, diminished, 397.
Reproduction,
  in amoeba, 293
  habits of birds, 347.
  sexual division in, 294, 346.
Resistance, synaptic,
  effect of, 329, 393.
  relative, 375.
Response,
  adequate, 49.
  anticipatory, 326.
  to unusual, 372, 382.
  to usual, 36.
Rhinal fissure, 98.
Rhinarium, 96.
Rhinencephalon, 106.
Rogers, 186.
Romanes, 98.

Scent, memories of, 109.
Semi-circular canals, 190.
Sense,
  chemical, 107.
  functioning in animals, 55
  of invertebrates, 86.
  olfactory, 88.
  organs, 37.
  stereognostic, 123.
Sensibility,
  deep and superficial, 120.
  epicritic, 122, 129, 334.
  protopathic, 121, 129, 334.
Sensitivity,
  development of, 357.
Sensory,
  area of cortex, 155.
  centres of vision, 46.
  decussation, 133.
  overlap, 236.
Sensory nerves, 12, 123.
  contribution to consciousness, 388.
Sex drive, 346.
Sherrington, 213, 284.
Sleep, 61.
  and conditioned repose, 390.
  ear folding in, 257.
  mechanism of, 389.
Smell,
  in aquatic animals, 66, 86.
  importance of, 96, 409.
Smith, Elliot, 154, 211.
Sound-colour combinations, 255.
Speech,
  development of, 409.
  importance of, 313.
  theories of origin, 409.
Spinal cord,
  issuing nerves, 12.
  tracts, 130.
Spino-thalamic tract, 132.
Spurzheim, 77, 208, 211.
Stimulus,
  appreciation of visual, 60.
  conducting of, 41.
  of pain and temperature, 131.
  prepotent, 336.
  recurring, 375.
  relevant, 51, 328.
  response to, 49.
Striatum, 218.
Sympathetic system (*see* Autonomic).
  action, 245.
  nerves, 239.
Synapses, 43.
  resistance at, 329.
Syndrome thalamique, 142.
Synergics, 200.

Tarsius, 147, 154, 278.
Taste,
  placodes of, 107.
Tendon,
  transplantation, 206.
Thalamic lesions, 142.
Thalamo-cortical fibres, 135.
Thalamus, 132, 135, 140, 219.
Thought, as motor response, 406.
Titubation, 194.
Touch, 131.
  sensitivity, 308.

Unlearned reactions, 304, 336.
  (*see* Instinctive reactions).
  complexity of, 342.
Unusual,
  response to, 372, 382.

Vertebrates,
  development of eye in, 29, 32.
  nervous system of, 28.
  reflexes in, 126.
Vertigo, 193.
Vibrissae, sensory, 88.
Vision,
  in goldfish, 52.
  monocular and binocular, 275, 276.
  photopic, 272.
  photostatic element, 263, 268.
  range of stimuli of, 38.
  scotopic, 269.

Walking mechanism, 222.
Washburn, 55.
Watson, J. B., 414.
Wilson, Kinnier, 186, 188.
Winslow, 239.

LINACRE COLLEGE LIBRARY
UNIVERSITY OF OXFORD

Jxt/JAR

~~6.50~~